Taxonomy, phylogeny and biogeography of Central European *Kybos* (Insecta: Hemiptera: Cicadellidae)

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Roland Mühlethaler

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auf Antrag von

Prof. Dr. Peter Nagel
PD Dr. Daniel Burckhardt
Prof. Dr. Hannelore Hoch

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Dekan
Prof. Dr. Hans-Peter Hauri

Contents

List of figures

List of tables

1 Introduction

Groups of phytophagous insects are ususally more species-rich than their non-phytophagous sister clades. Host shifts (= new ecological niches) as well as coevolution with their host plants have been advocated as underlying mechanism for this richness (Futuyma & Mitter, 1996; Price, 1997). Another independent factor triggering speciation is geographic vicariance and dispersal (Burckhardt & Ouvrard, 2007). For investigating these evolutionary models detailed knowledge of the taxonomic and phylogenetic relationships is required. Traditionally taxonomy was based on morphology which provides in most cases good characters for diagnosing species. In examples where morphology currently fails this is most often due to poor work rather than genuine absence of distinctive characters. In some cases diagnostic characters are known for one sex or one stage only, and association of females and nymphs with identified males is difficult. For some time now molecular techniques are in use, which potentially help defining species and associating different sexes and instars of the same species. A relatively new practice is the so called "DNA barcoding" which is using the mitochondrial COI sequence. The initial euphorism, however, was dampened by recent studies who demonstrated the unsuitability as the universal gene for discrimination of animal species (Tautz *et al*., 2003; Wheeler, 2005; Meier, 2006).

Within exopterygote insects, the Hemiptera constitutes with about 80,000-100,000 described species the most species-rich order. They belong to the "Big Five" (orders with around 100,000 and more species) of the global biodiversity. They are characterised by the unique sucking mouth parts for extracting liquids from plants, animals or fungi. They occupy a wide range of habitats although a majority is terrestrial and phytophagous. Only the suborder Heteroptera contains aquatic and carnivorous taxa. Unsurprisingly Hemiptera form a morphologically and biologically extremely diverse group (Carver, Gross & Woodward, 1991; Grimaldi & Engel, 2005; Hodkinson & Casson, 1991; Kristensen, 1991).

Traditionally the order Hemiptera comprises the suborders Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha and Heteroptera (Dolling, 1991). The probably paraphyletic Auchenorrhyncha with some 40,000 described species worldwide is composed of the two well supported monophyletic Fulgoromorpha and Cicadomorpha. Recent analyses of hemipteran phylogeny are still controversial (Cryan, 2005; Yoshizawa & Saigusa, 2001), though the Sternorryncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera are considered monophyletic by most authors (Bourgoin & Campbell, 2002; Dietrich, 2002; Nielson, 1985). Sorensen *et al.* (1995) proposed the formal classification with the suborders

Sternorrhyncha, Clypeorrhyncha (for extent Cicadomorpha), Archaeorrhyncha (for Fulgoromorpha) and Prosorrhyncha (for Coleorrhycha and Heteroptera).

Cicadomorpha can be distinguished from other Hemiptera by following characters: postclypeus enlarged; antennal pedicel small, without conspicuous sensilla, flagellum aristiform; tegulae absent; anal veins of forewing usually separated from base to apex; mesocoxae small and narrowly separated. According to Dietrich (2002) the Cicadomorpha comprises the cicadas (Cicadoidea), spittlebugs and froghoppers (Cercopoidea), as well as leafhoppers, sharpshooters and treehoppers (Membracoidea s.l.). He defines the superfamilies mainly with morphological characters, and estimates that about 6-10% of plant-feeding insects belong to the Cicadomorpha. To date, 30,000 species have been described in over 5,000 genera and 13 families. They feed either on phloem (Membracidae), on xylem (Cicadoidea, Cercopoidea and many Cicadellinae) or on parenchyma (Typhlocybinae). Many taxa of the superfamily Membracoidea are of economic importance. They transmit phytopathogenetic organisms causing plant diseases (Bourgoin & Campbell, 2002; Carver *et al.*, 1991; Dietrich, 2005; Kristensen, 1991; Nielson, 1985).

Cicadellidae is the largest family of Membracoidea with 50 subfamilies and 17,000-20,000 described species (Dolling, 1991; Hodkinson & Casson, 1991). Leafhoppers (Cicadellidae) live in all biogeographical regions and feed on a wide range of host plants, though individual species have often trophically and geographically restricted ranges. Eight subfamilies of Cicadellidae occur almost exclusively in the Australian Region, five in the Neotropics, five in the Palaearctics, one in the Nearctics and the rest is present in two or more biogeographical regions; thirteen are cosmopolitan (Dolling, 1991; Nielson, 1985).

Despite the economic importance, there are surprisingly many gaps in the knowledge on the taxomomy, phylogeny, life history and biology of cicadellids. Generally the species identification of Cicadomorpha is difficult due to their homogenous morphology, the huge number of species and the paucity of identification keys (Dietrich, 2005; Nielson, 1985).

Within the Cicadellidae one of the most advanced subfamilies is the Typhlocybinae with respect to morphology and biology. This subfamily is cosmopolitan and the morphology is remarkably uniform compared to other subfamilies of leafhoppers. The body size is small (2.0-5.5 mm), adults are always macropterous with reduced forewing venation lacking forks or cross-veins. Most species feed on leaf mesophyll cells of Dicotyledones. This is an evolutionary derived and specialised method of plant feeding causing white spots on leaves. The spots are in fact empty air-filled cells which can be seen on a variety of herbaceous plants. Exceptions are members of the tribe Empoascini feeding both on parenchyma and

phloem, and *Empoasca vitis* and *Jacobiasca libyca* on phloem only. Unlike other Cicadomorpha and Fulgoromorpha, Typhlocybinae lack secondary microbial endosymbionts. Parenchyma cells seem to contain all necessary nutrients (Dolling, 1991; Nickel, 2003; Nielson, 1985).

The eggs are laid with the ovipositor in slits in plant tissue. As most Hemiptera the Typhlocybinae have five nymphal instars. In cool or temperate regions the species hibernate as egg, nymph or adult. Depending on the climatic environment they produce one or more generations per year (Dolling, 1991; Nielson, 1985).

Mostly morphological characters of adults have been used for the classification of leafhoppers, e.g. the type, form and venation of the wings, the structure of the head, the position of the ocelli and the male genitalia. On tribal and generic levels the venation of the fore and hind wings are used (DeLong, 1971). Male genitalia and sound producing organs (apodemes) have been considered the only reliable characters for species separation. Identification keys are based on these characters (e.g. Ribaut, 1936; Le Quesne & Payne, 1981; Ossiannilsson, 1981). Closely related sympatric species are often difficult to separate by these characters for following reasons: the male genitalia are subjected to intraspecific variation which has, however, not been thoroughly examined in all species and some species have been described from a few males based on subtle genital differences only; the shape of the apodemes depends on the age of an individual which was not taken into consideration by some authors when describing new species. Data on host plant, behaviour and life history are still unknown for most species (Blocker & Triplehorn, 1985; Günthart, 1977; Nielson, 1985).

In the last decades bioacoustic techniques became increasingly important in insect taxonomy (Claridge, 2006). All leafhoppers and planthoppers produce substrate transmitted acoustic signals in contrast to the loud and prominent airborne songs of cicadas. Still little is known about the mechanisms of sound production in leafhoppers. Until the pioneer work of Ossiannilsson (1946, 1949) only the airborne calls of cicadas were known. With simple techniques he demonstrated that many species of leaf- and planthoppers produce sounds. Their calls consist usually of pulses with characteristic patterns of amplitude modulation. Male calls are normally more sophisticated than those of females. The vibrations are transmitted to the plant substrate through the tarsi and sometimes through the inserted stylets of the mouth. One of the main purposes of these so called songs is to attract and find mates for reproduction. Closely related species tend to differ clearly in their songs (Claridge, 2006; Cryan, 2005; Drosopoulos, 2006). In several different genera of Cicadellidae the taxonomy of

sibling species was clarified by song differences (Shaw, Vargo & Carlson, 1974; Claridge, 1985).

A good example to illustrate the taxonomic problems typical for Typhlocybinae is the genus *Empoasca* Walsh with some 500 described species. The genus is currently divided into three subgenera: *Empoasca* s.str., *Kybos* Fieber and *Kyboasca* Zachvatkin. The Holarctic subgenus *Kybos* comprises some 110 species, 42 of which are restricted to the Palaearctic Region. *Kybos* species are usually monophagous on *Salix*, *Populus, Alnus* or *Betula* spp. The taxonomy, phylogeny and biogeography of *Kybos* are mostly unknown. Many species have been described after single individuals and differences between some species are subtle. Only two papers (Ross, 1963; Dworakowska, 1976) deal with the taxonomy and phylogeny of *Kybos.* The monophyly of the genus *Empoasca* nor of any of its subgenera has been tested so far.

Here I revise the taxonomy and phylogeny of the Central European *Kybos* species. I investigate standard morphological (male genitalia, apodemes), molecular (the protein coding cytochrome c oxidase subunit I – COI – of the mitochondrial DNA and the ribosomal subunit rRNA – 16S) and bioacoustic methods for their taxonomic suitability. I examine females and last instar nymphs for taxonomically relevant characters. The improved taxonomic base is used for investigating host plant and biogeographical patterns.

2 Material and methods

2.1 Material examined

A total of 1098 specimens and 22 European *Kybos* species were examined (Appendix 1). Additionally six specimens of five Central Asian species and one specimen of an unidentified Nearctic *Kybos* species were added to the molecular data set. The closely related *E. vitis* (Göthe, 1875) and *K. bipunctata* (Oshanin, 1871) were used for outgroup comparison.

Seventeen *Kybos* species were collected and examined for the molecular studies. Totally 56 specimens and 23 species from different localities were examined (Appendix 1). Most of the insects were collected using a sweep net and an aspirator, stored in 96 % pure ethanol and identified by R.M. The samples of H. Nickel were collected in malaise traps and stored in 70% alcohol. As control and outgroup for the molecular analyses we chose the spittle bug *Philaenus spumarius* (L.) (Hemiptera, Cercopidae) taking the sequence data from GenBank.

2.2 Morphological studies

For the morphological studies dry mounted specimens from museum collections and freshly collected individuals were examined. For the observations of the genital structures with the light microscope the abdomen of fresh or dried specimens were removed and cleared in a solution of hot 10% KOH. After cleaning in distilled water and 70% alcohol the genitalia were stained with chlorazol black if necessary. Drawings and digital photographs of the genitalia were made in glycerin or glycerine-gelatine using a Leica DMLB light microscope. A camera lucida was used to produce drawings. The software Automontage (Syncroscopy®) was used to produce perfectly focused pictures with high resolution. The female abdomens used for SEM photographs were detached from the dried body and the abdominal sternite 7 was removed to render the base of the ovipositor visible. All SEM pictures were made at the Zentrum für Elektronenmikroskopie (ZBM, University Basel) with a scanning electron microscope Philips XL30 FEG.

The species descriptions and the identification key were made using the software DELTA (DEscription Language for TAxonomy), version 1.04 (Dallwitz, 1980; Paine & Zurcher, 1999). The morphological terminology follows Ossiannilsson (1978) and Davis (1975).

2.3 DNA sequences

We extracted mitochondrial DNA from specimens preserved in 96 % pure ethanol using a modification of the NaCl-extraction technique of Medrano, Aasen & Sharrow (1990). A 769bp sequence of the cytochrome oxidase I gene (COI), corresponding to positions 2265-3033 of the *Drosophila yakuba* mtDNA (Clary & Wolstenholme, 1985), was amplified using primers C1-J-1718 and C1-N-2191 (Nancy). A 388bp sequence of the 16S rRNA gene corresponding to positions 12295-12683 of the *D. yakuba* mtDNA (Clary & Wolstenholme, 1985), was amplified using primers N1-J-12261 and LR-N-12945 (N116S). The specimens sequenced for each of the mtDNA regions are listed in Appendix 1. The PCR reactions were performed in a MJ Research PTC-100 thermal cycler. The optimized temperature profile for the COI fragment consisted of 35 cycles of 30 s denaturation at 95°C, 1 min annealing at 40°C, a further 30 s annealing at 50°C and 2 min extension at 72°C. For the 16S rRNA–tRNAlue(CUN)–ND1 fragment the temperature profile consisted of 35 cycles of 30 s denaturation at 95°C, 30 s annealing at 47°C and 90 s extension at 72°C. In both cases there was an initial denaturation step of 2 min at 95°C. The PCR products were checked for size and lack of multiple bands by agarose gel electrophoresis and purified with the Wizard PCR Preps DNA Purification System (Promega) according to the manufacturer's protocols. Sequences were determined directly, in both the 5' and 3' directions, using the same primers as above. Sequencing was either manual, using the Sequenase Version 2.0 DNA Sequencing Kit (United States Biochemical/ Amersham International plc.) and 35S dATP (Du Pont NEN) with autoradiographic visualization, or automated, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA Polymerase, FS (Perkin Elmer) with separation on an ABI PRISM 377 DNA Sequencer (Perkin Elmer). Sequences were aligned using Sequencher (Gene Codes Corporation Inc., Ann Arbor, Michigan), CLUSTAL X version 1.83 (Thompson *et al.*,1997) and DNAMAN version 6 (Lynnon Corporation, Quebec). Comparison with the *D. yakuba* mtDNA from the GenBank suggested that the sequence fragments were from functional COI and 16S rRNA genes and no missense mutations or stop codons were detected. All sequences will be available at GenBank after publication.

2.4 Bioacoustic analyses

All acoustic studies were made at the National Institute of Biology (NIB) in Ljubljana (Slovenia). For song recording the animals were placed in the laboratory on small branches of

their fresh host plants. A small reflector was glued on the stem and the vibratory signals were recorded with a commercial laser vibrometer (Polytec system with the OFV-303 sensor head, OFV-300 modular vibrometer controller, OVD-02 velocity and OVD-20 displacement decoders; Polytech GmbH, Waldbrün, Germany) and stored directly on a notebook with an appropriate soundcard. Simultaneously the behaviour was observed. Further analyses of the songs have been made using the software Cool Edit Pro version 2.0 (Adobe Systems Inc., San Jose, CA) and GoldWave version 5.04 (GoldWave Inc., St. John's, Canada).

2.5 Phylogenetic analyses

For the morphological cladistic analysis a data matrix was produced (Table 2) with 19 species of *Kybos* and one species each of the outgroups *Kyboasca* and *Empoasca* respectivly. Sixteen characters were chosen (Table 1). Character states were marked as dashes (–) if inapplicable and as question marks (?) if ambiguous or missing (Table 2). Three characters relate to the wings, seven to the male gentialia, five to the female genitalia and one to the nymphs. The morphological cladistic analysis was performed with NoNa (Goloboff, 1999) using the interface WinClada version 1.00.08 (Nixon, 2002). Multistate characters were treated as unorderd (= non additive), all characters were assigned equal weights. A heuristic search was performed with following settings: maximum trees to keep = 10000; number of replications = 5; starting trees per replication = 5; search strategy = multiple tbr + tbr. The Nelsen command was used to calculate a consensus tree. For mapping the characters onto the consensus cladogram (Fig. 18), the fast character optimization was used.

PAUP*4.10 (Swofford, 1998) was used to perform the molecular cladistic analyses. *Philaenus spumarius* (Cercopidae) was added as an outgroup (GB accession number AY630340). In order to investigate genetic divergences and possible saturation effects that could interfere with later phylogenetic analysis, an initial neighbor joining analysis using uncorrected (p) and corrected (K2P) genetic distances, which corrects for differences in transition and transversion ratios, was performed. The commonly used Kimura two-parameter model of substitution (K2P) was employed on the basis that more sophisticated models do not necessarily result in better phylogenetic inference (Nei & Kumar, 2000). Branch support was assessed by 1000 nonparametric bootstrap replicates (Felsenstein, 1985).

3 Results

3.1 Taxonomy

3.1.1 Morphological character assessement

Coloration. Adult: Face usually greenish, sometimes ranging to yellowish as in *K. abstrusus* and *K. populi*, or rarely fuscous as in *K. sordidulus*. Pronotum and scutellum greenish or brownish, bearing often a few white spots or a white longitudinal band in the middle (e.g. *K. lindbergi*, *K. populi*, *K. smaragdula* or *K. virgator*). Fore wing generally greenish; commisural border sometimes concolorous with remainder of wing (e.g. *K. populi*) or with a brown band (e.g. *K. rufescens*, *K. butleri*); colour of corioclaval suture either concolorous with remainder of wing (e.g. *K. populi*) or bearing a black spot or fuscous (e.g. *K. smaragdula*). Abdomen greenish, in some species with darker and stronger pigmented tergites. Teneral specimens pale and weakly pigmented. With a few exceptions (*K. rufescens*, *K. sordidulus*) the coloration does not diagnose *Kybos* species. – Nymph: Body colour variing from green, with hardly any markings, to brownish. Posterior margins of abdominal tergites often brown.

Sexual characters. Male (Fig. 1): The aedeagus is, by far, the most important structure for diagnosing *Kybos* species. Appendages absent (e.g. *K. rufescens*, *K. populi*) or present (e.g. *K. lindbergi*, *K. virgator*); where present, divergent from (e.g. *K. virgator*) or parallel to the main stem (e.g. *K. lindbergi*); length variing from shorter than (e.g. *K. lindbergi*) to as long as main stem (e.g. *K. austriacus*); base of appendages broad and widely separated in the middle (e.g. *K. lindbergi*) or almost contiguous (e.g. *K. virgator*). There are some species where the appendages of some individuals may bear irregular spines or teeth (prominent e.g. in *K. strigilifer*); this character is very variable and not diagnostic. Pygofer process apically slender in all Central European species except for *K. populi* where it is broadened. Processes of anal collar either short and stout (e.g. *K. lindbergi*, *K. smaragdula*) or long and slender (e.g. *K. rufescens*, *K. virgator*). A further taxonomically important character is the shape of the male singing organs, the apodemes. This structure is only fully developed after a few days of hatching and caution is required with teneral specimens where the apodemes are usually shorter. Length of apodemes of sternite II variing from shorter than broad to twice as long as broad; length of phragma lobes of tergit III variing from shorter than broad to longer than broad.– Female: Sternite VII in all European species bearing prolongated lobe, except for *K. populi* where it is equally rounded. Three types of shape of the ovipositor base can be distinguished: 1. wider than long (e.g. *K. smaragdula*), 2. as long as broad as in *K. lindbergi*

or 3. longer than wide as in *K. populi*; distal edge straight (e.g. *K. mucronatus*), equally rounded as in *K. smaragdula* or with an incision (e.g. *K. populi*).

3.1.2 Morphological species concept

As shown in the character assessment the aedeagus is the single most important structure for diagnosing species. The second good diagnoser is the shape of the sound apodemes, teneral specimens excluded.

Kybos virgator (Figs. 7D-E) and *volgensis* (Figs. 7F-G) are morphologically similar and differ only in the shape of the apodemes. The two taxa are sympatric and are both associated with willows. In the surroundings of Basel (Switzerland) and Moravia (Czech Republic) individuals of *K. volgensis* were observed only during a few days in June and August respectively, whereas those of *K. virgator* were registered during a few weeks. A few specimens with intermediate apodeme shape were collected. These observations are more consistant with *K. volgensis* representing a juvenile apodeme form of *K. virgator* than the occurrence of two biologically seperated species. *K. volgensis* is, therefore, synonymised here with *K. virgator*.

K. perplexus (Figs. 3C-D) was separated from *strigilifer* (Figs. 3A-B) by the aedeagal appendages bearing spines. Günthart (1974) showed with breeding experiments that the presence of spines is highly variable within *strigilifer*. Dworakowska (1976), interpreting Günthart's data slightly differently, concluded that the two are separate species. In the material at hand from several Central and Northern European countries (Appendix 1) we observed a significant variability in this structure. The two forms share the same distribution and occur together. In the surroundings of Basel (Switzerland) the two were collected together on the same tree. These observations are in accord with Günthart's conclusions can be best interpreted as intraspecific variation with respect to aedeagal appendages. For this reason *K. strigilifer* and *perplexus* are here synonymised.

A third type of taxonomic problem is illustrated by *K. lindbergi* and *K. ludus* (Figs. 7S-U), a species pair associated with birch. They are morphologically similar but differ subtly in the shape of the aedeagal appendages. *K. ludus* occurs in Western Europe, *K. lindbergi* in Northern and Eastern Europe. In Germany and Switzerland the two species are sympatric and intermediate morphological forms are frequent. Based on the available evidence we conclude that *K. lindbergi* and *K. ludus* are distinct, geograpically separated species which are sympatric in a relatively restricted area in Central Europe, where hybridisation occurs. The name *K. ludus* is used here according to Hamilton (1983) who suggested that this is a senior

synonym of *Empoasca* (*Kybos*) *betulicola*. This was followed by della Giustina (1989). Based on the original description and illustration of *K. ludus* by Davidson & DeLong (1938) Nickel (2003) and other European workers rejected this synonymy. We have examined the holotype of *K. ludus* which clearly shows that it is conspecific with *K. betulicola.* We agree with Hamilton and reject the use of the name *K. betulicola.*

3.1.3 Species descriptions

***Kybos* Fieber**

Kybos Fieber, 1866: 508; type species *Cicada smaragdula* Fallén, 1806, by monotypy; Nast, 1972; Le Quesne, 1981.

Empoasca Walsh, 1862: 149, p.p.; Horváth, 1897, with *Kybos* as junior synonym.

Empoasca (*Kybos*) DeLong, 1931: 14; Metcalf, 1968; Dworakowska, 1976; Ossiannilsson, 1981.

Host plant range. Betulaceae (*Alnus*, *Betula*) and Salicaceae (*Populus*, *Salix*).

Distribution. Holarctic; Eurasia 45 species, North America 78 species.

***Kybos abstrusus* (Linnavuori)** (Figs. 2A-B, 5A, 6A, 8A)

Empoasca abstrusa Linnavuori, 1949: 148.

Kybos topoli Zachvatkin, 1953a: 209; synonymised by Dworakowska, 1976.

Body length. Male 4.2-4.7 mm; female 4.5-4.9 mm.

Coloration. Adult: Face greenish or yellowish; commisural border concolorous with remainder of fore wing; corioclaval suture concolorous with forewing.

Sexual characters. Male: Aedeagus without processes. Pygofer process slender apically. Process of anal collar long and slender. Apodemes of sternite II twice as long as broad; phragma lobes of tergit 3 shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view narrow and angular, without a median ridge, hook-shaped distally.

Host plant. Populus nigra.

Distribution. Austria, Bulgaria, Finland, France (mainland), Germany, Hungary, Lithuania, Poland, Romania, central part of European Russia, Sweden, Switzerland, Ukraine, former Yugoslavia.

***Kybos aetnicola* Wagner, 1959** (Figs. 2K, 4A, 5B, 6B)

Kybos aetnicola Wagner, 1959: 81.

Body length. Male: 4.4-4.5 mm; female: 4.5-4.8 mm; nymph: 2.8 mm.

Coloration. Adult: Face greenish; commisural border concolorous with fore wing; corioclaval suture black or fuscous. – Nymph: Green, almost with hardly any markings, posterior margins of abdominal tergits brown.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view, ventral to main stem; length of processes as long as stem; basis of processes close to each other. Pygofer process in male slender apically. Process of anal collar short and stout. – Female: Sternite VII with prolongated lobe.

Host plant. Betula aetnensis.
Distribution. Italy (Mt. Etna, Sicily).

***Kybos austriacus* (Wagner, 1949)** (Figs. 2L-M, 8F)
Empoasca austriaca Wagner, 1949: 43.

Body length. Male: 4.2-4.5 mm; female: 4.7-4.8 mm.
Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous.
Sexual characters. Male: Aedeagus with parallel sited processes, in lateral view parallel to main stem; length of processes as long as stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded, with a median ridge, distally straight.
Host plant. Betula spp.
Distribution. Austria, Switzerland.

***Kybos butleri* (Edwards, 1908)** (Figs. 2C, 4B, 5C, 6C, 8B, 11B)
Empoasca butleri Edwards, 1908: 82.
Kybos oshanini occidentalis Zachvatkin, 1953a: 208; synonymised by Dworakowska, 1976.
Empoasca ovalis Ross, 1963: 217; synonymised by Dworakowska, 1976.

Body length. Male 3.9-4.3 mm; female 4.2-4.7 mm; nymph 3.5 mm.
Coloration. Adult: Face greenish; commisural border of fore wing with a brown band; corioclaval suture concolorous with forewing. – Nymph: brown pattern on pro-, meso- and metanotum, tergit 2 with two dark spots, posterior margins of abdominal tergits brown.
Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad; phragma lobes of tergit III as long as broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view narrow and angular; without a median ridge; distally hook-shaped; apex of median valvula bearing 6-10 teeth; structure of teeth regular triangular; ventral edge of valvula apically evenly curved.
Nymph. Length of tibia 3 distinctly shorter than half of body length (<0.4).
Host plant. Salix aurita, S. cinerea, S. repens, S. triandra. S. caprea, S. myrsinifolia.
Distribution. Belgium, Denmark (mainland), Estonia, Finland, France (mainland), Germany, Great Britain, Greece (mainland), Hungary, Italiy (mainland), Latvia, Lithuania, Netherlands, Poland, North part of European Russia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, former Yugoslavia.

***Kybos calyculus* (Cerutti, 1939)** (Figs. 2N-O, 4C, 5D, 6D)
Empoasca calycula Cerutti, 1939: 92.
Kybos studzinskii Dworakowska, 1973: 239; synonymised by Dworakowska, 1976.

Body length. Male 4.1-4.3 mm; female 4.2-4.4 mm.
Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous.
Sexual characters. Male: Aedeagus with divergent processes, in lateral view ventraly of main stem, length of processes shorter than stem, basis of processes close to each other.

Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III as long as broad or shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded; with a median ridge; distally straight.

Host plant. Betula pubescens.

Distribution. Czech Republic, Germany, Great Britain, Poland, Switzerland.

***Kybos candelabricus* Dlabola, 1958** (Figs 2P, 4D, 5E, 6E)
Kybos candelabricus Dlabola, 1958: 331.

Body length. Male: 4.7-5.0 mm; female: 4.8-5.1 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view parallel to main stem, length of processes as long as stem; basis of processes widely apart from each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe.

Host plant. Salix spp.

Distribution. Bulgaria, Georgia, Turkey (Anatolia).

***Kybos digitatus* (Ribaut, 1936)** (Figs. 2Q-R, 4E, 5F, 6F, 9D)
Empoasca digitata Ribaut, 1936: 178.

Body length. Male 3.7-3.9 mm; female 3.9-4.4 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous.

Sexual characters. Male: Aedeagus with parallel sited processes, in lateral view dorsaly of main stem; length of processes shorter than stem; basis of processes widely apart from each other. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad; phragma lobes of tergit III as long as broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded; without a median ridge; distally rounded.

Host plant. Salix elaeagnos.

Distribution. France (mainland), Germany, Switzerland.

***Kybos limpidus* (Wagner, 1955)** (Figs. 2D-E, 4F, 5G, 6G, 8C, 11D)
Empoasca limpida Wagner, 1955: 176.

Body length. Male 4.2-4.4 mm; female 4.8-5.1 mm; nymph 2.9-3.2 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture concolorous with forewing. – Nymph: Light green, almost without any markings.

Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view narrow and angular; without a median ridge; distally hook-shaped; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically evenly curved.

Nymph. Length of tibia 3 distinctly shorter than half of body length (<0.4).

Host plant. Salix viminalis, S. triandra, possibly *S. pentandra*.
Distribution. Czech Republic, Germany, Hungary, Netherlands, Poland, Ukraine.

***Kybos lindbergi* (Linnavuori, 1951)** (Figs. 2T-U, 4G, 5H, 6H, 9A, 11C)
Empoasca lindbergi Linnavuori, 1951: 60.
Empoasca borealis Lindberg, 1952: 144; synonymised by Linnavuori, 1953.
Kybos betulae (sic!) Zachvatkin, 1953a: 206; synonymised by Nast, 1972
Empoasca austriaca Ossiannilsson, 1955: 131 (nec Wagner, 1949).

Body length. Male 4.2-4.4 mm; female 4.6-4.8 mm; nymph 2.9 mm.
Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous. – Nymph: Light green, almost without any markings, only posterior margins of abdominal tergits brown.
Sexual characters. Male: Aedeagus with parallel sited processes, in lateral view parallel to main stem; length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad or as long as broad; phragma lobes of tergit III as long as broad or shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge, distally straight; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically strongly curved.
Nymph. Length of tibia 3 almost half of body length.
Host plant. Betula pendula, B. pubescens. B. nana.
Distribution. Czech Republic, Estonia, Finland, Germany, Kazakhstan, Latvia, Norway (mainland), Poland, central part of European Russia, Sweden, Switzerland, Ukraine.

***Kybos ludus* (Davidson & DeLong, 1938)** (Figure 2S)
Empoasca luda Davidson & DeLong, 1938: 94.
Empoasca betulicola Wagner, 1955: 178; synonymised by Hamilton, 1983.

Body length. Male 4.2-4.4 mm; female 4.6-4.8 mm; nymph 2.9 mm.
Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous. – Nymph: Green, almost without any markings, only posterior margins of abdominal tergits brown.
Sexual characters. Male: Aedeagus with parallel sited processes, in lateral view parallel to main stem, length of processes shorter than stem, basis of processes widely apart from each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad, or as long as broad, phragma lobes of tergit III as long as broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded, with a median ridge, distally straight; apex of median valvula bearing 6-10 teeth, structure of teeth irregular coarse, ventral edge of valvula apically strongly curved.
Nymph. Length of tibia 3 almost half of body length.
Host plant. Betula pendula, B. pubescens.
Distribution. Germany, Great Britain, Mongolia, Netherlands, south part of European Russia, Switzerland.

***Kybos mesasiaticus* (Zachvatkin, 1953)** (Figs. 2F, 4H, 5J, 6J, 11E)
Kybos oshanini mesasiaticus Zachvatkin, 1953a: 208.
Kybos mesasiaticus Zachvatkin, 1953b: 237.

Body length. Male: 3.8-4.2 mm; female: 3.8-4.2 mm

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture concolorous with forewing.

Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad; phragma lobes of tergit III longer than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view narrow and angular, without a median ridge, distally hook-shaped; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically evenly curved.

Host plant. Salix songorica.

Distribution. Dagestan, Mongolia, Kazakhstan, Kirghizia, south part of European Russia, Uzbekistan.

***Kybos mucronatus* (Ribaut, 1933)** (Figs. 2V-W, 4K, 5K, 6K, 10A)
Empoasca mucronata Ribaut, 1933: 151.
Kybos mucronatus verbae Zachvatkin, 1953a: 207.
Kybos cracoviensis Dworakowska, 1973: 239; synonymised by Dworakowska, 1976.

Body length. Male 4.6-4.7 mm; female 5.0 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view ventraly of main stem; length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad or as long as broad, phragma lobes of tergit III as long as broad or shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge; distally straight.

Host plant. Alnus glutinosa, reported also from *A. incana* and *Salix* spp.

Distribution. Czech Republic, France (mainland), Germany, Latvia, Poland, central part of European Russia, Slovenia, Switzerland, former Yugoslavia.

Comment. Nickel (2003) discussed the synonymy of *verbae* with *mucronatus.* Here we follow Nickel.

***Kybos paraltaicus* Orosz, 1996**
Empoasca paraltaica Orosz, 1996: 153.

Body length. Male 4.3 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous.

Sexual characters. Male: Aedeagus with divergent processes, length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad; phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe.

Host plant. Unknown.

Distribution. Hungary.

Comment. K. paraltaicus is known from a single male from Hungary only. Additional material is necessary for elucidating its identity.

***Kybos populi* (Edwards, 1908)** (Figs. 2G, 4K, 5L, 6L, 8D, 11F)
Empoasca populi Edwards, 1908: 81.
Kybos populi tremulae Zachvatkin, 1953a: 208; synonymised by Dworakowska, 1976.
Kybos zaisanensis Mitjaev, 1968: 635; synonymised by Dworakowska, 1976.

Body length. Male 3.8-4.5 mm; female 4.0-4.7 mm; nymph 3.2.

Coloration. Adult: Face greenish, or yellowish; commisural border of fore wing concolorous; corioclaval suture concolorous with forewing. – Nymph: Light green, almost without any markings.

Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically broadend. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII without prolongated lobe, equally rounded; base of first valvifer in ventral view narrow and angular without a median ridge, distally straight; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically evenly curved.

Nymph. Length of tibia III distinctly shorter than half of body length (<0.4).

Host plant. Populus alba, *P. nigra*, *P. suaveolens*, *P. tremula.*.

Distribution. Austria, Belgium, Bulgaria, Czech Republic, Danish mainland, Estonia, Finland, France (mainland), Germany, Great Britain, Hungary, Italy (mainland and Sicily), Kazakhstan, Latvia, Republic of Moldova, Morocco, Netherlands, Norway (mainland), Poland, south part of European Russia, central part of Siberia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, former Yugoslavia.

***Kybos rufescens* Melichar, 1896** (Figs. 2H, 6M, 8E, 11G, 13B)
Kybos smaragdula (sic!) *rufescens* Melichar, 1896: 180.

Body length. Male 3.9-4.5 mm; female 4.1-4.6 mm.

Coloration. Adult: Face greenish; commisural border of fore wing brown band; corioclaval suture concolorous with forewing.

Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view narrow and angular without a median ridge, distally hook-shaped; apex of median valvula bearing 6-10 teeth, structure of teeth irregular coarse; ventral edge of valvula apically evenly curved.

Host plant. Salix purpurea, possibly *S. caesia*.

Distribution. Austria, Belgium, Bulgaria, Czech Republic, Danish mainland, French mainland, Germany, Great Britain, Hungary, Italy (mainland and Sicily), . Kazakhstan, Netherlands, Mongolia, Poland, Romania, south part of European Russia, Sardinia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, former Yugoslavia.

***Kybos smaragdula* (Fallén, 1806)** (Figs. 3H, 4L, 5M, 7A, 9B, 10B, 11H, 13E)
Cicada smaragdula Fallén, 1806: 37.
Empoasca smaragdula; Horváth, 1897: 45.
Kybos smaragdulus; Fieber, 1866: 508.

Body length. Male 3.8-4.3 mm; female 4.1-4.6 mm; nymph 3.6 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous. – Nymph: Light green, almost without any markings, only posterior margins of abdominal tergits brown.

Sexual characters. Male: Aedeagus with parallel sited processes, in lateral view parallel to main stem or dorsaly of main stem; length of processes shorter than stem; basis of processes widely apart from each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II shorter than broad; phragma lobes of tergit III as long as broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge, distally straight; apex of median valvula bearing 6-10 teeth; structure of teeth regular triangular; ventral edge of valvula apically strongly curved.

Nymph. Length of tibia 3 almost half of body length.

Host plant. Alnus glutinosa, A. incana, possibly *A. alnobetula.*

Distribution. Altai Mts., Armenia, Austria, Belgium, Bulgaria, Croatia, Czech Republic, Denmark (mainland), Estonia, Finland, France (mainland), Germany, Great Britain, Hungary, Ireland, Italy (mainland), Kazakhstan, Latvia, Lithuania, Netherlands, Norway (mainland), Poland, Portugal (mainland), Romania, central and north parts of European Russia, Sakhalin, Siberia, Slovakia, Slovenia, Spane (mainland), Sweden, Switzerland, Tadzhikistan, Ukraine, Uzbekistan, former Yugoslavia.

***Kybos sordidulus* (Ossiannilsson, 1941)** (Figs. 2J, 4M, 5N, 7B)
Empoasca sordidula Ossiannilsson, 1941: 69 (male); Ossiannilsson, 1942: 114 (female).
Empoasca (*Kybos*) *alaskana* Ross, 1963: 219; synonymised by Dworakowska, 1976.

Body length. Male 4.0-4.7 mm; female 4.0-4.7 mm.

Coloration. Adult: Face fuscous; commisural border of fore wing concolorous; corioclaval suture concolorous with forewing.

Sexual characters. Male: Aedeagus without processes. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III longer than broad. – Female: Sternite VII with prolongated lobe.

Host plant. Salix caprea, S. myrsinifolia, S. purpurea. S. phylicifolia.

Distribution. Finland, Norway (mainland), central part of European Russia, Sweden.

***Kybos strigilifer* (Ossiannilsson, 1941)** (Figs. 1A-F, 3A-D, 4N, 5O, 7C, 9E, 12A, 13C)
Empoasca strigilifera Ossiannilsson, 1941: 198.
Empoasca perplexa Ribaut, 1952: 459; syn. n.
Kybos altaicus Mitjaev, 1963: 66; synonymised with *Empoasca perplexa* by Dworakowska, 1976.

Body length. Male 3.9-4.3 mm; female 4.2-4.5 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view parallel to main stem; length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge, distally rounded; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically strongly curved.

Host plant. Salix caprea, S. cinerea, S. myrsinifolia.

Distribution. Austria, Belgium, Czech Republic, Danish mainland, Estonia, Finland, France (mainland), Germany, Great Britain, Ireland, Latvia, Lithuania, Norway (mainland), Poland, central and northern part of European Russia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, former Yugoslavia.

Comment. *K. perplexus* (Figs. 3C-D) is a younger synonym of *K. strigilifer*. The two species differ only in details of the aedeagal appendages. *K. perplexus* is reported from Belgium, France (mainland), Germany, Poland, Switzerland and Ukraine. *K. strigilifer* is not recorded for Belgium.

***Kybos strobli* (Wagner, 1949)** (Figs. 3E-G, 4O, 9C, 12B)
Empoasca strobli Wagner, 1949: 44.

Body length. Male 4.0-4.6 mm; female 4.0-4.6 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view dorsaly of main stem; length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar short and stout. Length of apodemes of sternite II shorter than broad; phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge, distally straight; apex of median valvula bearing 6-10 teeth; structure of teeth regular triangular; ventral edge of valvula apically strongly curved.

Host plant. A. incana, possibly on other *Alnus* spp.

Distribution. Austria, Czech Republic, Germany, Hungary, Italy (mainland), Poland, Slovenia, Switzerland, Ukraine.

***Kybos virgator* (Ribaut, 1933)** (Figs. 3J-O, 4P, 5P, 7D-G, 9F, 12C, 13F)
Empoasca virgator Ribaut, 1933: 152.
Empoasca virgator v. *saageri* Wagner, 1935: 28.
Kybos volgensis Vilbaste, 1961: 318; syn. n.

Body length. Male 4.0-4.5 mm; female 4.2-4.8 mm.

Coloration. Adult: Face greenish; commisural border of fore wing concolorous; corioclaval suture black or fuscous.

Sexual characters. Male: Aedeagus with divergent processes, in lateral view parallel to main stem; length of processes shorter than stem; basis of processes close to each other. Pygofer process in male apically slender. Process of anal collar long and slender. Length of apodemes of sternite II twice as long as broad, phragma lobes of tergit III shorter than broad. – Female: Sternite VII with prolongated lobe; base of first valvifer in ventral view broad and irregulary rounded with a median ridge; distally rounded; apex of median valvula bearing 6-10 teeth; structure of teeth irregular coarse; ventral edge of valvula apically evenly curved.

Host plant. Salix spp.; in Central Europe mainly on *Salix alba* and *S. fragilis*.

Distribution. Austria, Belgium, Bulgaria, Czech Republic, Danish mainland, Finland, France (mainland), Germany, Great Britain, Greece (mainland), Hungary, Italy (mainland), Kazakhstan, Latvia, Lithuania, Republic of Moldova, Mongolia, Netherlands, Norway (mainland), Poland, Romania, central part of European Russia, Sardinia, Slovakia, Sweden, Switzerland, Ukraine, former Yugoslavia.

Comment: Here we synonymise *K. volgensis* and *K. virgator*. The differences of the length of the apodemes are a result of teneral specimens (Figs. 7F-G). *K. volgensis* is reported from the South part of European Russia, Sweden and Switzerland.

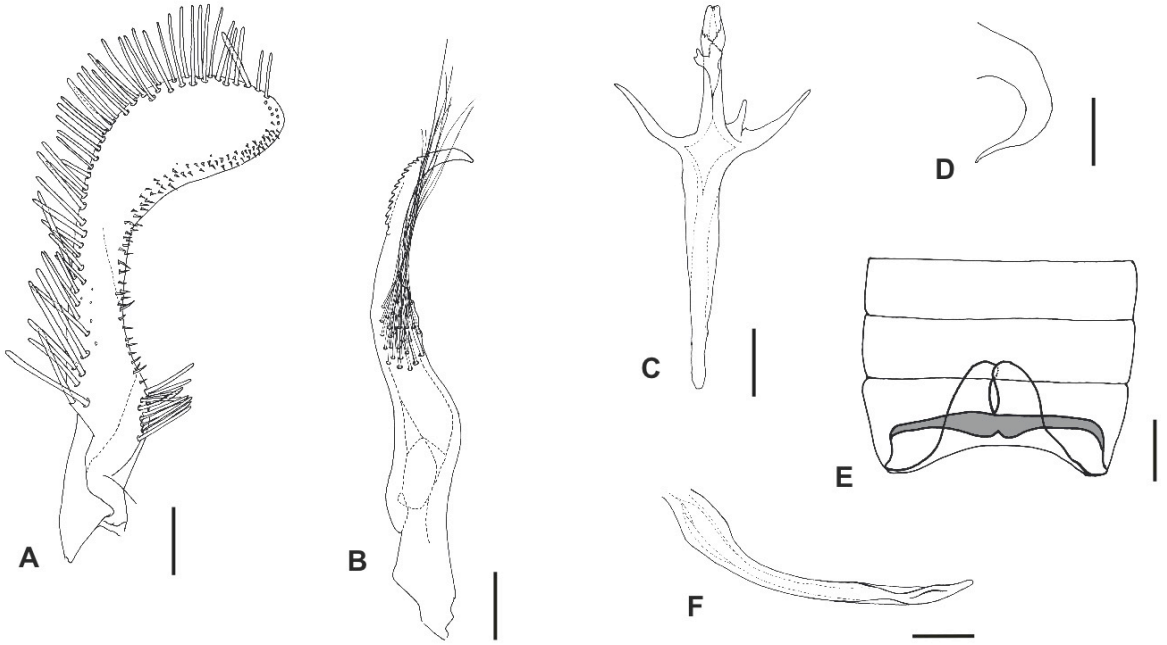

Figure 1. A-F, male genitalia of *Kybos strigilifer*. A, genital plate; B, stylus: C, aedeagus, ventral view; D, anal collar; E, apodemes (Aaodemes of tergit II in grey); F; pygofer. Scale bars: A-D, F = 0.1 mm; E = 0.2 mm.

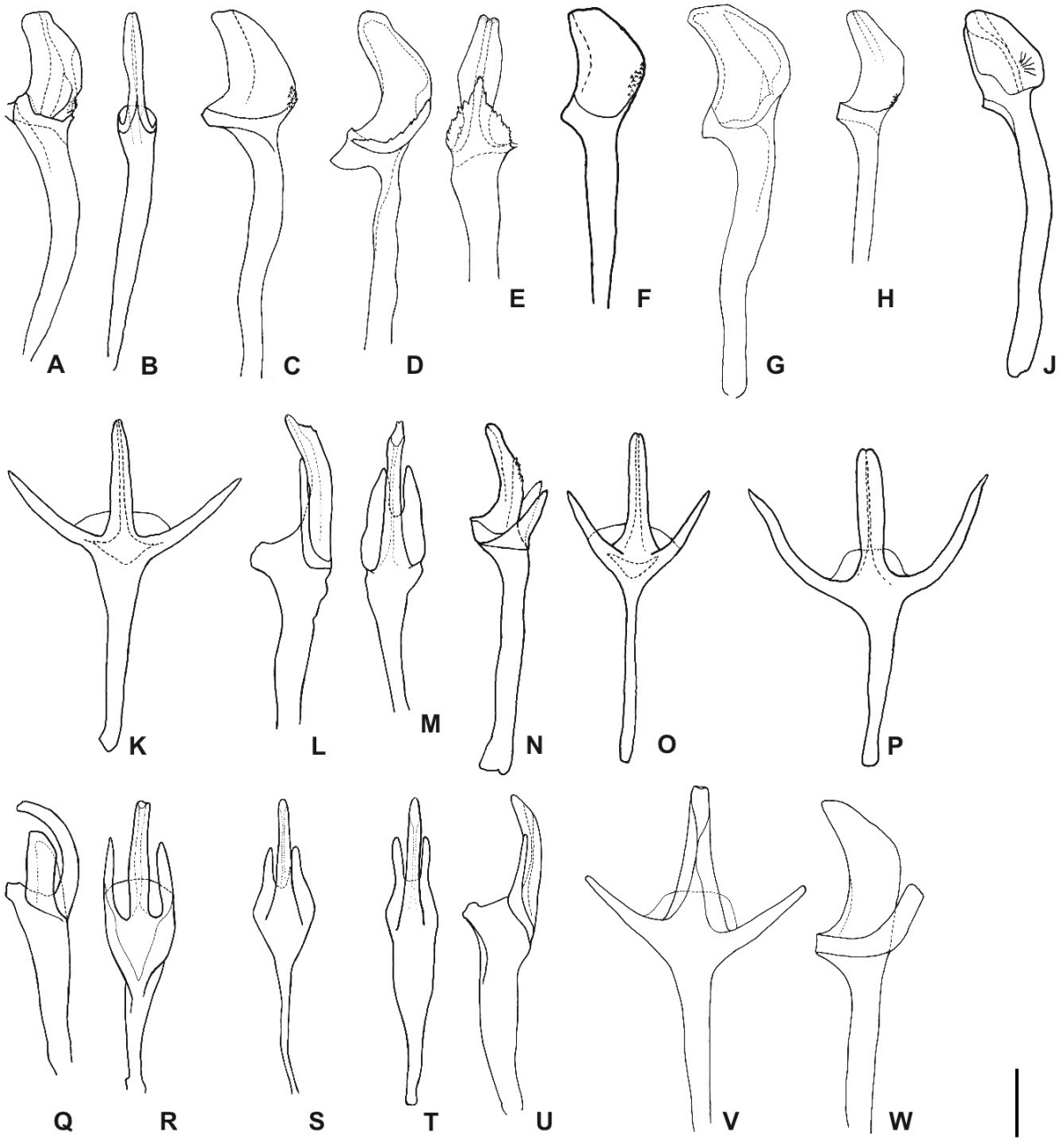

Figure 2. A-W, aedeagi of *Kybos* spp. A, *Kybos abstrusus*, lateral view; B, *K. abstrusus*, ventral view; C, *K. butleri*, lateral view; D, *K. limpidus*, lateral view; E, *K. limpidus*, ventral view; F, *K. mesasiaticus*, lateral view; G, *K. populi*, lateral view; H, *K. rufescens*, lateral view; J, *K. sordidulus*, lateral view; K, *K. aetnicola*, ventral view; L, *K. austriacus*, lateral view; M, *K. austriacus*, ventral view; N, *K. calyculus*, lateral view; O, *K. calyculus*, ventral view; P, *K. candelabricus*, ventral view; Q, *K. digitatus*,lateral view; R, *K. digitatus*, ventral view; S, *K. ludus*, ventral view; T, *K. lindbergi*, ventral view. U, *K. lindbergi*, lateral view; V, *K. mucronatus*, ventral view; W, *K. mucronatus*, lateral view. Scale bar = 0.1 mm.

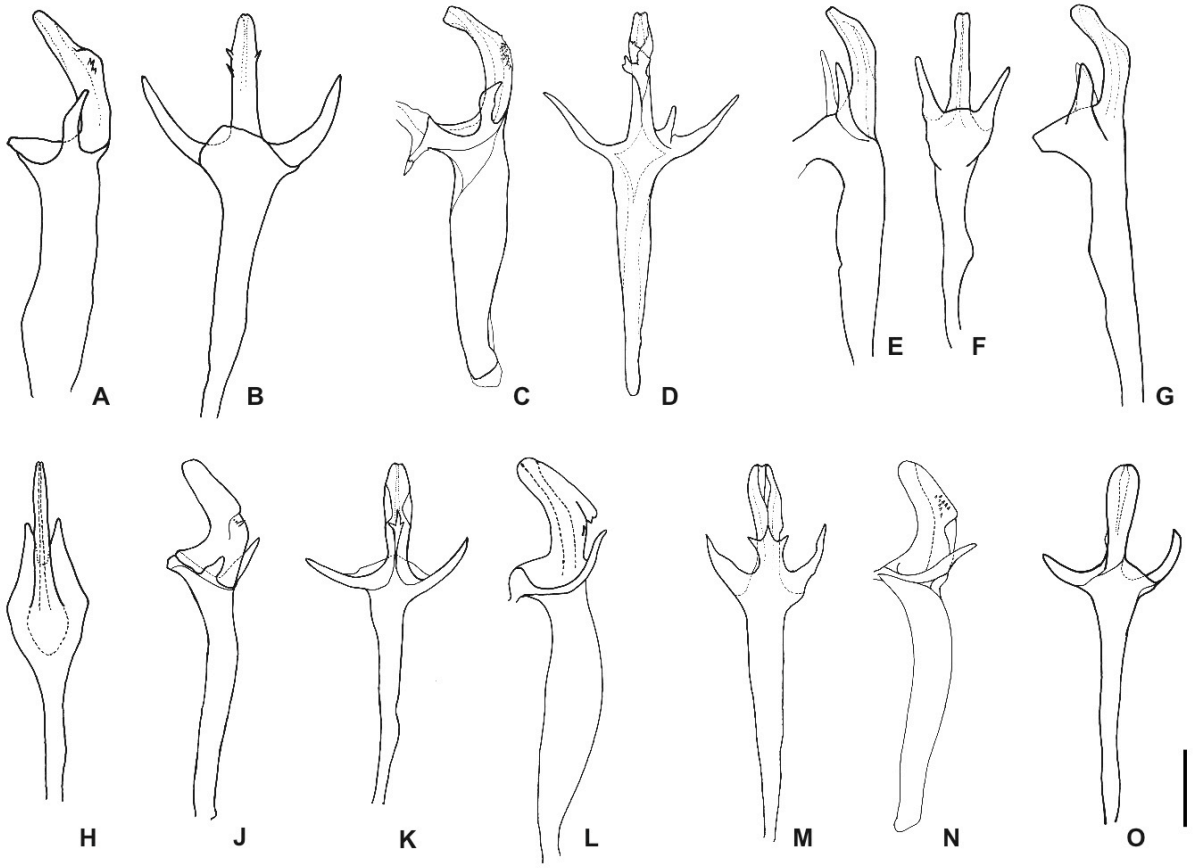

Figure 3. A-O, aedeagi of *Kybos* spp. A, *Kybos strigilifer,* lateral view; B, *K. strigilifer*, ventral view; C, *K. strigilifer* (*"perplexus"*), lateral view; D, *K. strigilifer* (*"perplexus"*), ventral view; E, *K. strobli*, lateral view; F, *K. strobli*, ventral view; G, *K. strobli*, lateral view; H, *K. smaragdulus*, ventral view; J, *K. virgator*, lateral view; K, *K. virgator*, ventral view; L, *K. virgator*, specimen from Slovakia, lateral view; M, *K. virgator*, specimen from Slovakia with some abberations, ventral view; N, *K. virgator*, same specimens as in M, lateral view; O, *K. virgator* (*"volgensis"*).
Scale bar = 0.1 mm.

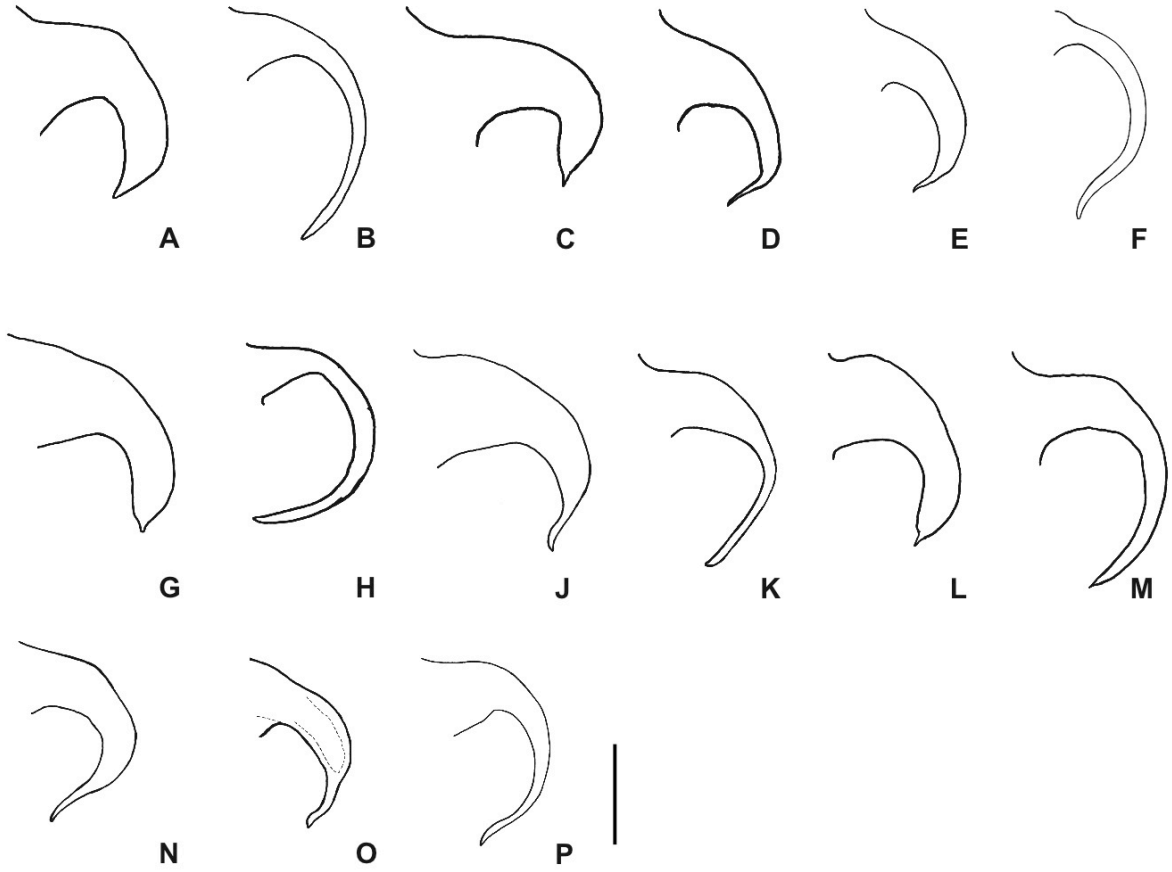

Figure 4. A-P, anal collar of *Kybos* spp. A, *Kybos aetnicola*; B, *K. butleri*; C, *K. calyculus*; D, *K. candelabricus*; E, *K. digitatus*; F, *K. limpidus*; G, *K. lindbergi*; H, *K. mesasiaticus*; K, *K. mucronatus*; K, *K. populi*; L, *K. smaragdulus*; M, *K. sordidulus*; N, *K. strigilifer*; O, *K. strobli*; P, *K. virgator*. Scale bar = 0.1 mm.

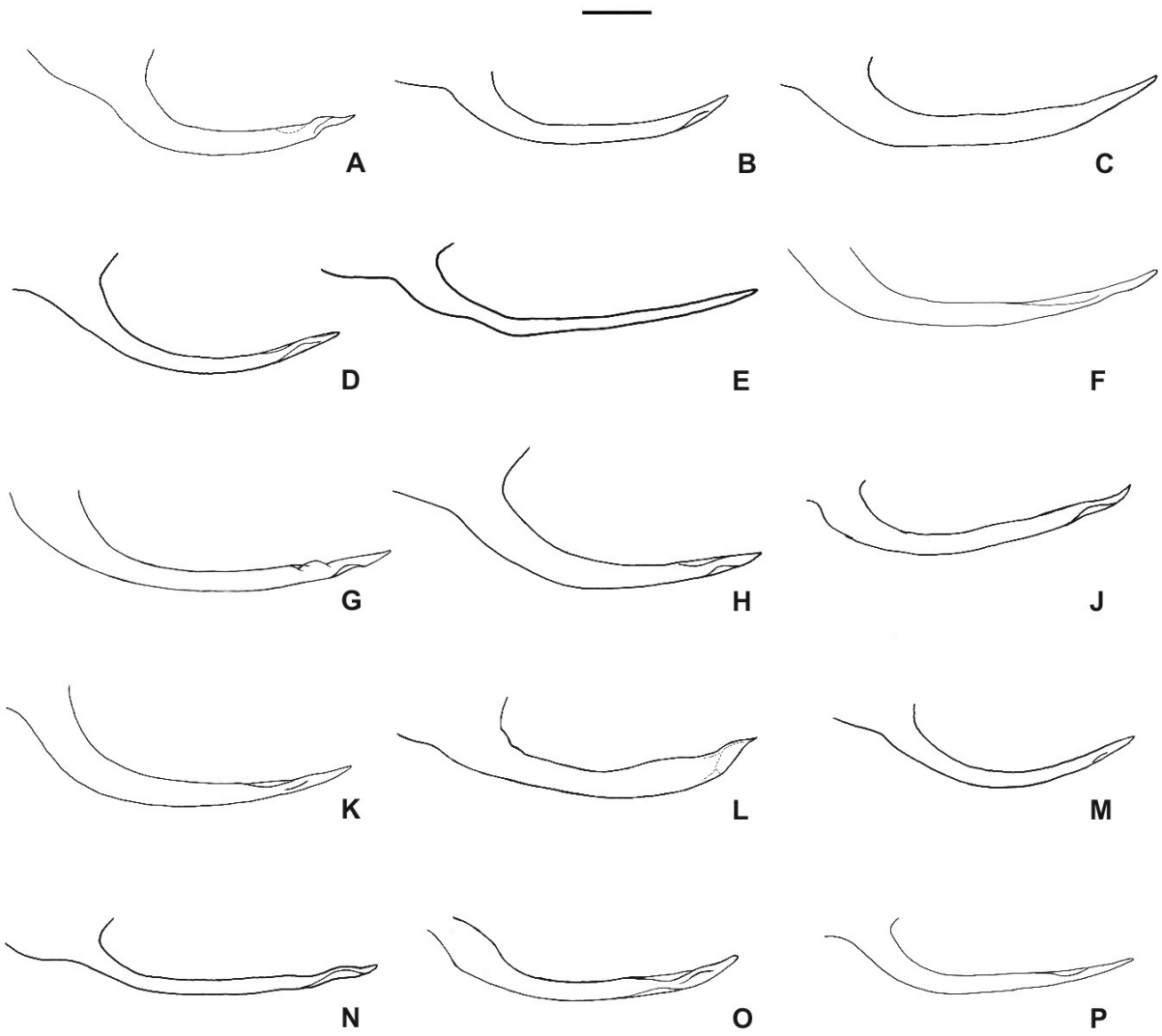

Figure 5. A-P, pygofer of *Kybos* spp. A, *Kybos abstrusus*; B, *K. aetnicola*; C, *K. butleri*; D, *K. calyculus*; E, *K. candelabricus*; F, *K. digitatus*; G, *K. limpidus*; H, *K. lindbergi*; J, *K. mesasiaticus*; K, *K. mucronatus*; L, *K. populi*; M, *K. smaragdulus*; N, *K. sordidulus*; O, *K. strigilifer*; P, *K. virgator*. Scale bar = 0.1 mm.

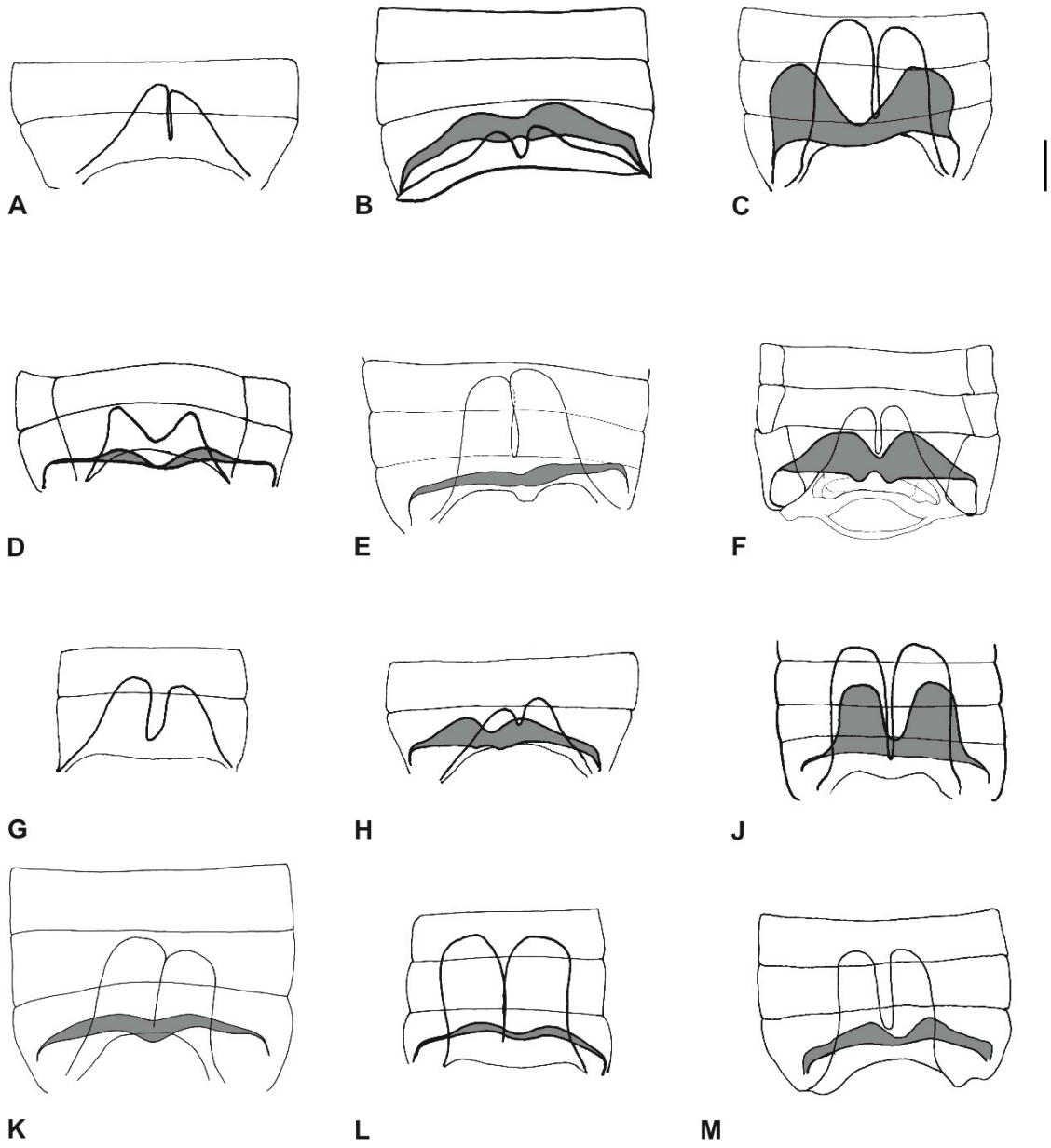

Figure 6. A-M, apodemes of *Kybos* spp. A, *Kybos abstrusus*; B, *K. aetnicola*; C, *K. butleri*; D, *K. calyculus*; E, *K. candelabricus*; F, *K. digitatus*; G, *K. limpidus*; H, *K. lindbergi*; J, *K. mesasiaticus*; K, *K. mucronatus*; L, *K. populi*; M, *K. rufescens*. Scale bar = 0.2 mm.

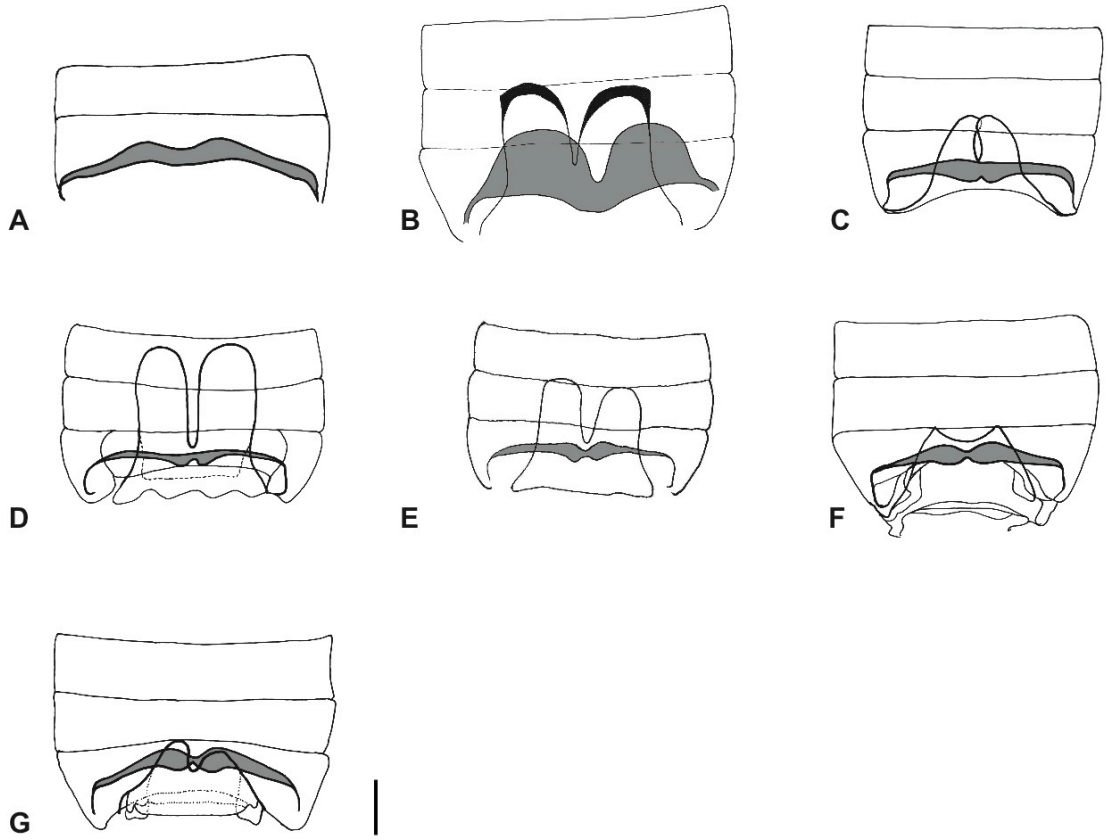

Figure 7. A-E, apodemes of *Kybos* spp. A, *K. smaragdulus*; B, *K. sordidulus*; C, *K. strigilifer*; D, *K. virgator*; E, *K. virgator*, intermediate specimen; F, *K. virgator*, teneral specimen; G, *K. virgator*, teneral specimen. Scale bar = 0.2 mm.

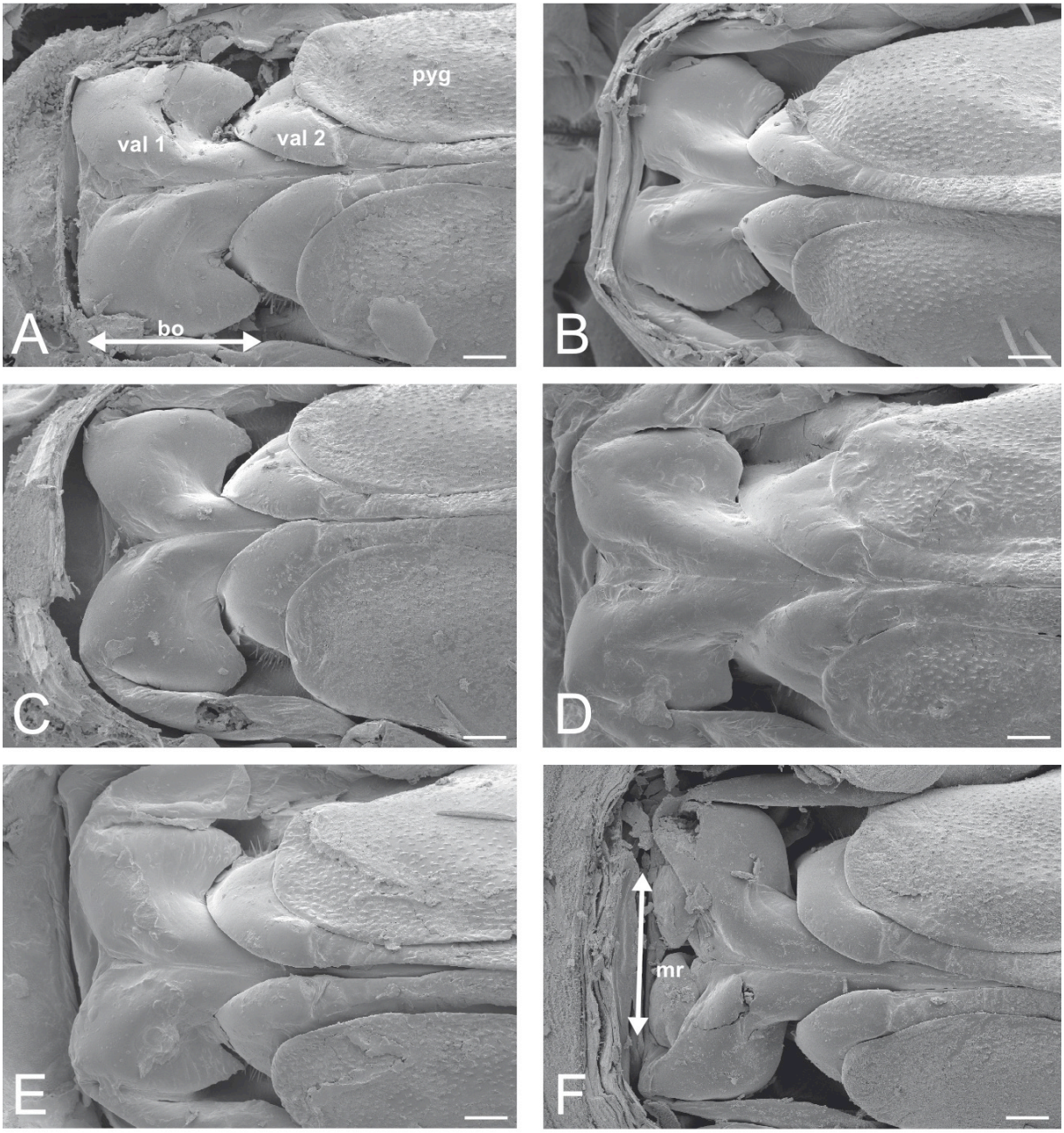

Figure 8. A-F, base of ovipositors of *Kybos* spp. (ventral view). A, *Kybos abstrusus*; B, *K. butleri*; C, *K. limpidus*; D, *K. populi*; E, *K. rufescens*; F, *K. austriacus*. Abbreviations: bo, base of ovipositor; mr, median ridge; pyg, pygofer; val 1, first valvifer; val 2, second valvifer. Scale bars = 50 µm.

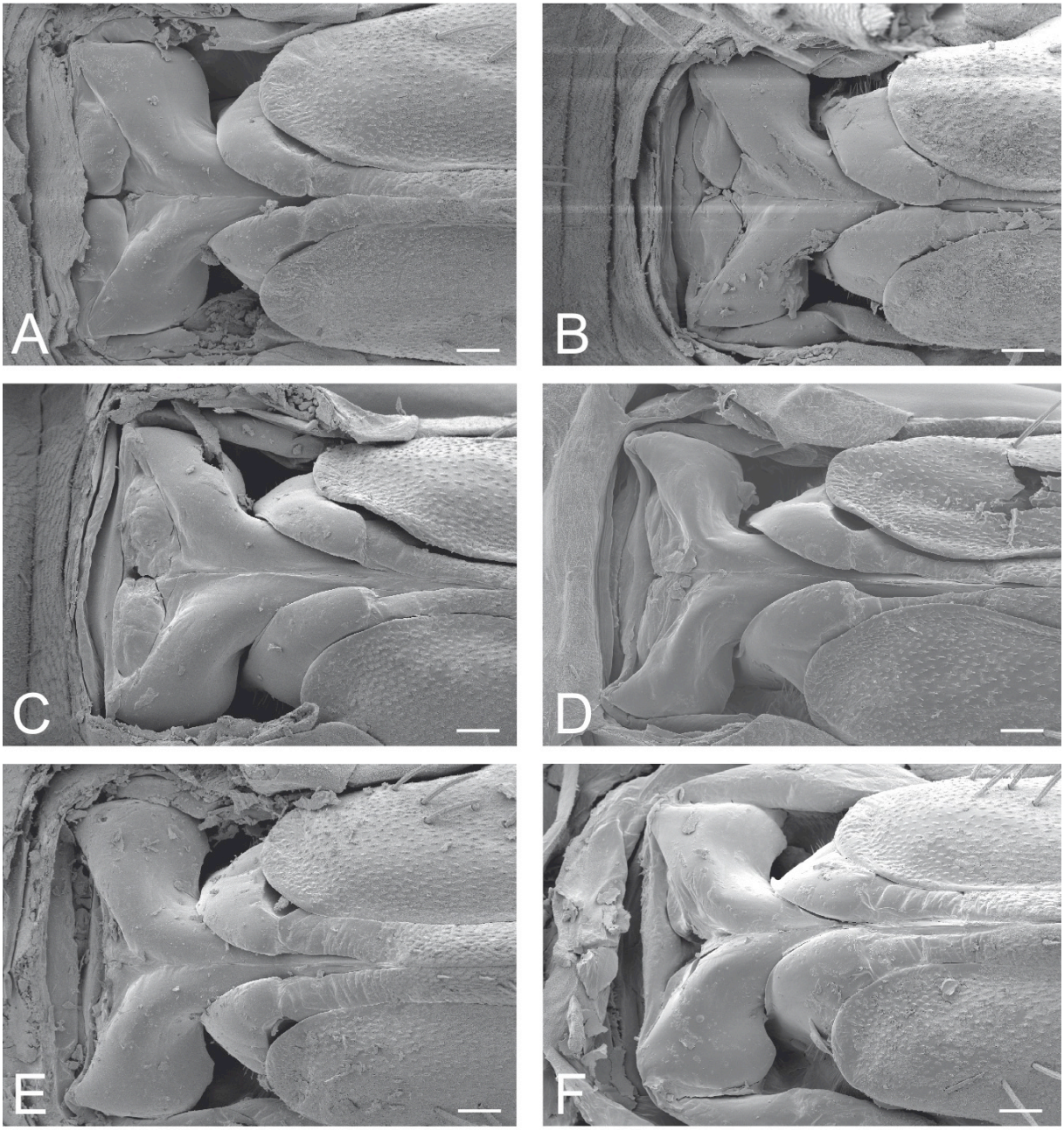

Figure 9. A-F, base of ovipositors of *Kybos* spp. (ventral view). A, *Kybos lindbergi*; B, *K. smaragdula*; C, *K. strobli*; D, *K. digitatus*; E, *K. strigilifer*; F, *K. virgator*. Scale bars = 50 µm.

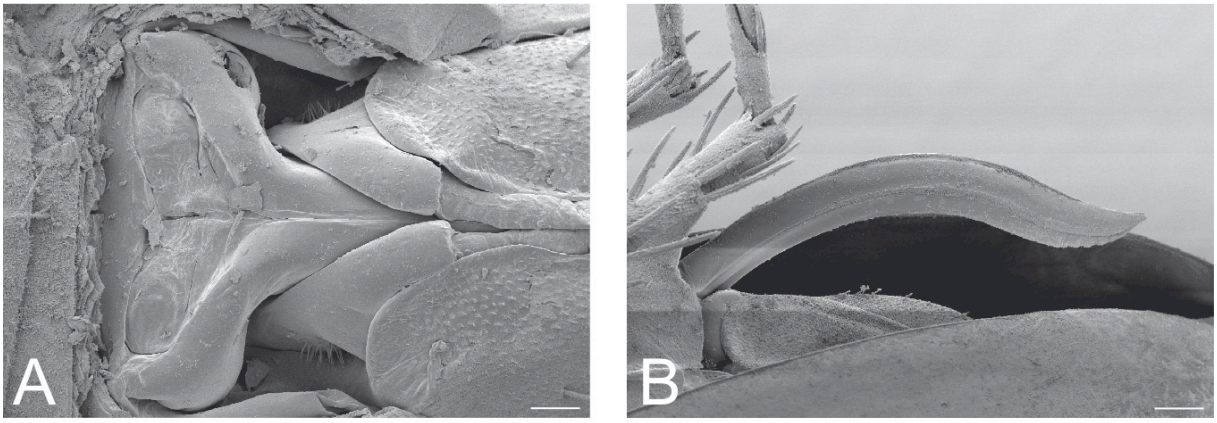

Figure 10. A, *Kybos mucronatus*, base of ovipositors (ventral view); B, *K. smaragdula*, ovipositor (lateral view). Scale bars: A = 50 μm, B = 100 μm.

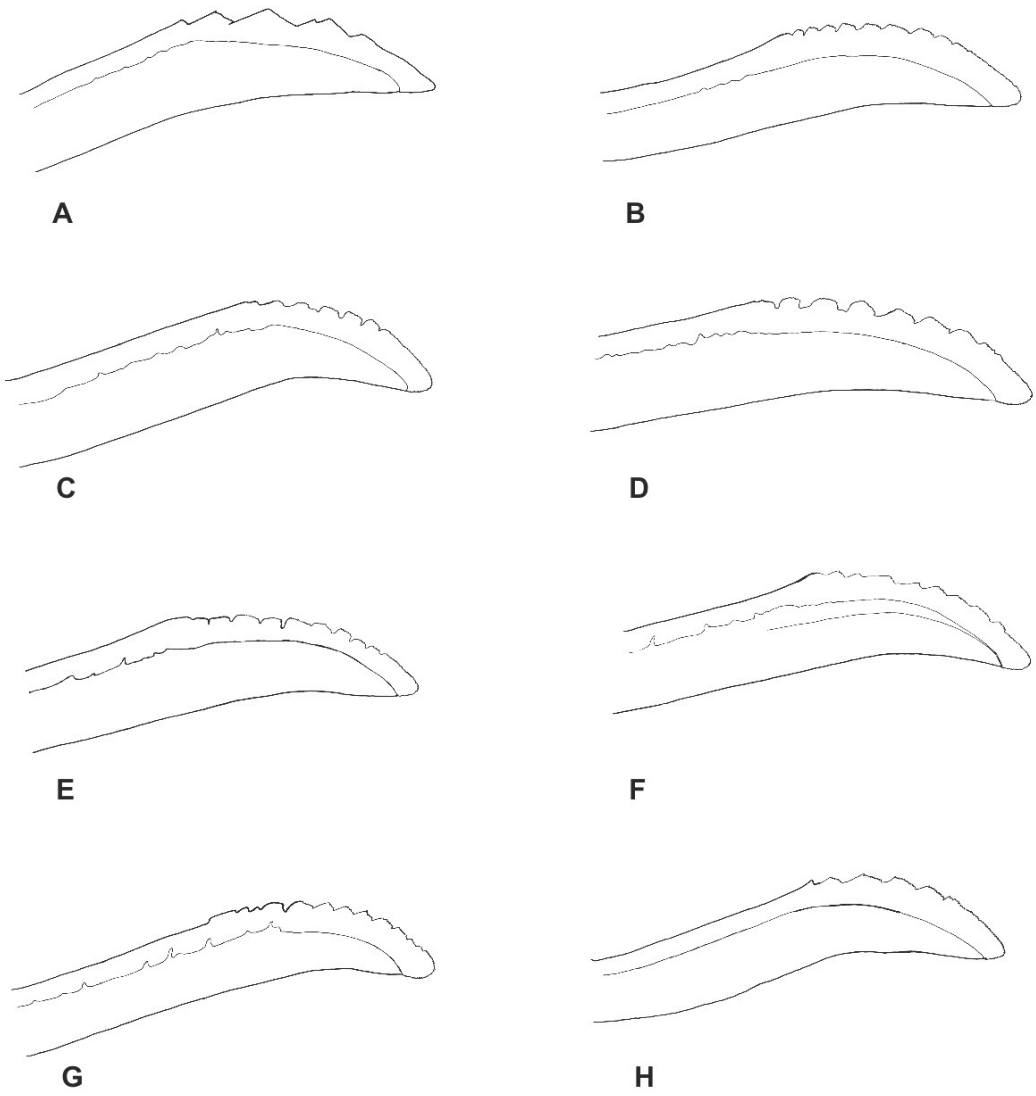

Figure 11. A-H, apex of valvifer (lateral view). A, *Kyboasca bipunctata*; B, *Kybos butleri*; C, *Kybos lindbergi*; D, *Kybos limpidus*; E, *Kybos mesasiaticus*; F, *Kybos populi*; G, *Kybos rufescens*; H, *Kybos smaragdulus*. Scale bar = 0.1 mm.

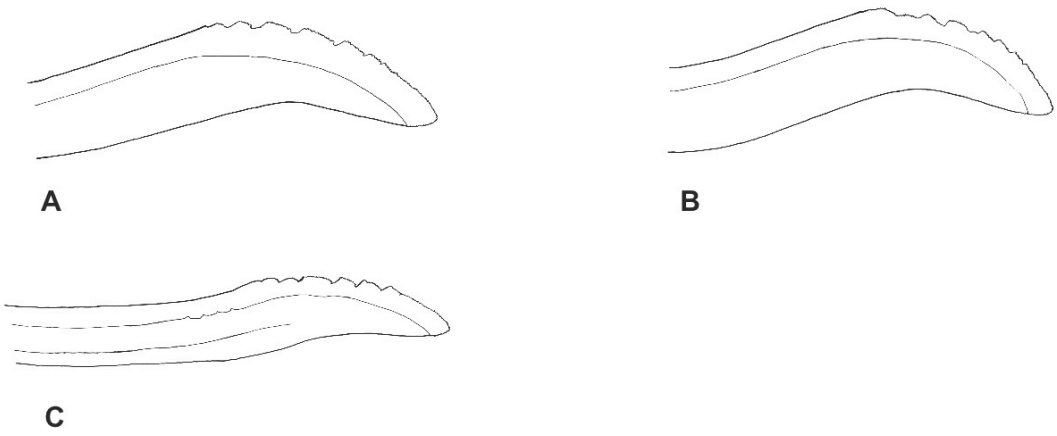

Figure 12. A-C, apex of valvifer (lateral view). A, *Kybos strigilifer*; B, *Kybos strobli*; C, *Kybos virgator*. Scale bar = 0.1 mm.

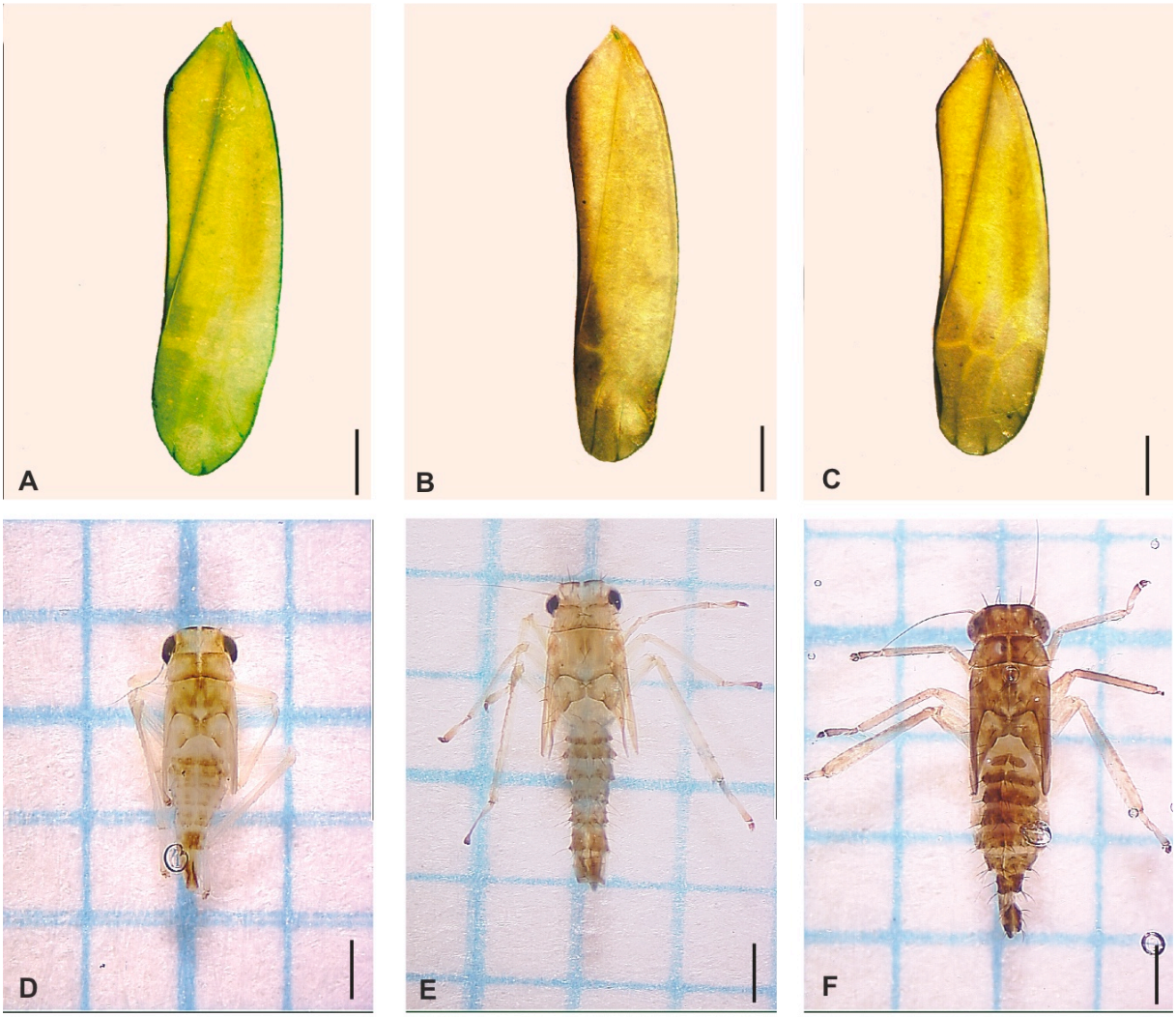

Figure 13. A-C, colour patterns of forewings of *Kybos* spp. A, *Kybos lindbergi*; B, *Kybos rufescens*; C, *Kybos strigilifer*; D-F, nymphs of *Kybos* spp. D, *Kybos limpidus*; E, *Kybos smaragdulus*; D, *Kybos virgator.* Scale bars = 0.5 mm.

3.1.4 Key to *Kybos* species

1 Male 2
Female 20
2(1) Colour of commisural border of fore wing concolorous 3
Colour of commisural border of fore wing bearing a brown band 19
3(2) Colour of face fuscous ..... ***sordidulus***
Colour of face greenish or yellowish 4
4(3) Aedeagus without appendages 5
Aedeagus with appendages 8
5(4) Pygofer process in male broadend apically (Fig. 5L) ..... ***populi***
Pygofer process in male slender apically 6
6(5) Aedeagal stem, in profile, thick. On *Populus* spp. ..... ***abstrusus***
Aedeagal stem, in profile, slender. On *Salix* spp. 7
7(6) Aedeagus bearing conspicuous spines ventrally (Fig. 2E); phragma lobes of tergit 3 shorter than broad (Fig. 6G). On *Salix viminalis* ..... ***limpidus***
Aedeagus without conspicuous spines ventrally; phragma lobes of tergit 3 longer than broad (Fig. 6J). ..... ***mesasiaticus***
8(4) Aedeagus with parallel-sided appendages 9
Aedeagus with divergent appendages 13
9(8) Basis of appendages of aedeagus widely apart from each other 10
Basis of appendages of aedeagus close to each other 12
10(9) Process of anal collar long and slender (Fig. 4E). On *Salix eleagnos* ..... ***digitatus***
Process of anal collar short and stout (e.g. Fig. 4L). On *Alnus* spp. or *Betula* spp. 11
11(10) Length of apodemes of sternite II as long as broad or longer. On *Betula* spp. ..... ***ludus***
Length of apodemes of sternite II shorter than broad. On *Alnus* spp. ..... ***smaragdula***
12(9) Aedeagal appendages broad and almost as long as stem (Fig. 2M) ..... ***austriacus***
Aedeagal appendages slender and shorter than stem (Fig. 2T) ..... ***lindbergi***
13(8) Process of anal collar very long and slender (Fig. 4P) ..... ***virgator***
Process of anal collar short and stout (e.g. Figs. 4A, 4C, 4O) 14
14(13) Aedeagal appendages strongly curved in ventral view (Fig. 2P) ..... ***candelabricus***
Aedeagal appendages straight in ventral view (e.g. Figs. 2K, 2O, 3A) 15
15(14) Aedeagal appendages, in ventral view, as long as stem (Fig. 2K) ..... ***aetnicola***
Aedeagal appendages, in ventral view, distinctly shorter than stem 16
16(15) Length of apodemes of sternite II longer than broad (Figs. 6D, 7C) 17
Length of apodemes of sternite II shorter than broad (e.g. Fig. 6K) 18
17(16) Aedeagal appendages, in lateral view, ventral of main stem. On *Betula* spp. ..... ***calyculus***
Aedeagal appendages, in lateral view, parallel to main stem. On *Salix* spp. ..... ***strigilifer***
18(16) Aedeagal appendages, in lateral view, parallel to main stem, blunt apically (Fig. 2W) ..... ***mucronatus***
Aedeagal appendages, in lateral view, dorsal of main stem, pointed apically (Fig. 2G) ..... ***strobli***
19(1) Length of phragma lobes of tergit III shorter than broad (Fig. 6M) ..... ***rufescens***
Length of phragma lobes of tergit III longer than broad, clearly separated medially, diverging (Fig. 6C) ..... ***butleri***
20(1) Colour of commisural border of fore wing bearing a brown band 21
Colour of commisural border of fore wing concolorous 22
21(20) Outer margin of base of first valvifer distinctly angular (Fig. 8B) ..... ***butleri***
Outer margin of base of first valvifer weakly rounded (Fig. 8E) ..... ***rufescens***
22(20) Base of first valvifer, in ventral view, narrow, angular, straight distally, bearing a median transverse ridge (e.g. Fig. 8F) 23

Base of first valvifer, in ventral view, broad, irregulary rounded, often hook-shaped distally, lacking a median transverse ridge (e.g. Fig. 8A, 8D)..... 26
23(22) Apex of median valvula bearing obliquely triangular teeth (e.g. Figs. 11H, 12 B). On *Alnus* spp. 24
Apex of median valvula bearing irregular, blunt teeth (e.g. Figs. 11C, 12C). On *Betula* spp. or *Salix* spp..... 25
24(23) Apex of median valvula weakly curved ..... ***mucronatus***
Apex of median valvula strongly curved (Figs. 11H, 12B)..... ***smaragdula, strobli***
25(23) On *Betula* spp..... ***austriacus***, ***calyculus***, ***lindbergi***, ***ludus***
On *Salix* spp. ..... ***candelabricus***, ***digitatus***, ***strigilifer***, ***virgator***
26(22) Base of first valvifer, in ventral view, angular distally. Sternite VII without a prolongated lobe, evenly rounded (Fig. 8D). 27
Base of first valvifer, in ventral view, hook-shaped distally. Sternite VII with a prolongated lobe (Figs. 8A, 8C) 28
27(26) On *Populus* spp. ..... ***populi***
On *Salix* spp. ..... ***sordidulus***
28(26) On *Populus nigra* ..... ***abstrusus***
On *Salix* spp. ..... ***limpidus***, ***mesasiaticus***

3.1.5 Molecular evidence

There are no COI or 16S sequences available at GenBank for *Kybos* or other members of the Empoascini. The cytochrome c oxidase subunit I (COI) of the mitochondrial DNA is often used to investigate the relationships of closely related species. This essentially non-recombining genome, inherited only by the mother, leads to shorter coalescence times (Sperling, 2003). COI has been proposed as the gene for barcoding animals (Hebert *et al*., 2003).

COI sequences were obtained for 46 specimens and 16S sequences for 51 specimens. For the analyses only these specimens were retained where both, COI and 16S sequences were obtained. We sequenced 769 bp for COI and 388 bp for 16S. The base frequencies over all are: A=0.33084, C=0.12960, G=0.13396, T=0.40560.

We aligned the raw COI and 16S sequences manually (excluding highly length-variable regions) and analysed the aligned sequences separately and together (Appendices 2-3).

Following species are composed of genetically homogeneous specimens with identical or almost identical COI sequences: *mucronatus* + *strigilifer/perplexus* + *virgator/volgensis*, *calyculus*, *digitatus*, *smaragdula* (except sample 1449 which is closer to the group of *mucronatus*/*strigilifer*/*virgator*). Of particular interest are the identical sequences of *K. virgator*/*volgensis* from the same locality. This corroborates the conclusions drawn from morphological evidence that the two are synonyms. *K. strigilifer*/*perplexus* from the same locality are identical, but are also identical with the sequences of *mucronatus* and *virgator*. With respect to the synonymy of *strigilifer* and *perplexus* the molecular data do neither

support nor contradict morphological evidence. In the case of *K. lindbergi* and *ludus* the sequences are similar but not identical. The molecular data is not conclusive but does not contradict the morphological evidence.

The situation is quite different in *K. butleri* and *K. rufescens*. The former consists of two well defined genotypes (Figs. 14-15), the latter shows an unusually large genetic variation (Fig. 16). In both species neither morphology nor host plant association suggest that there may be cryptic species involved. The two genotypes of *K. butleri* cannot be attributed to distribution as both samples contain specimens from different localities. It is of importance to note that the two genotypes do not consist of the same specimens regarding COI and 16S. The specimens 1415/1498, respectively 1305/1496/1497 represent the two genotypes in COI, whereas in 16S sequences 1305/1498, respectively 1415/1496/1497 form the two separated genotypes.

Generally the 16S sequences show less differences than COI and are therefore less informative for the taxonomy.

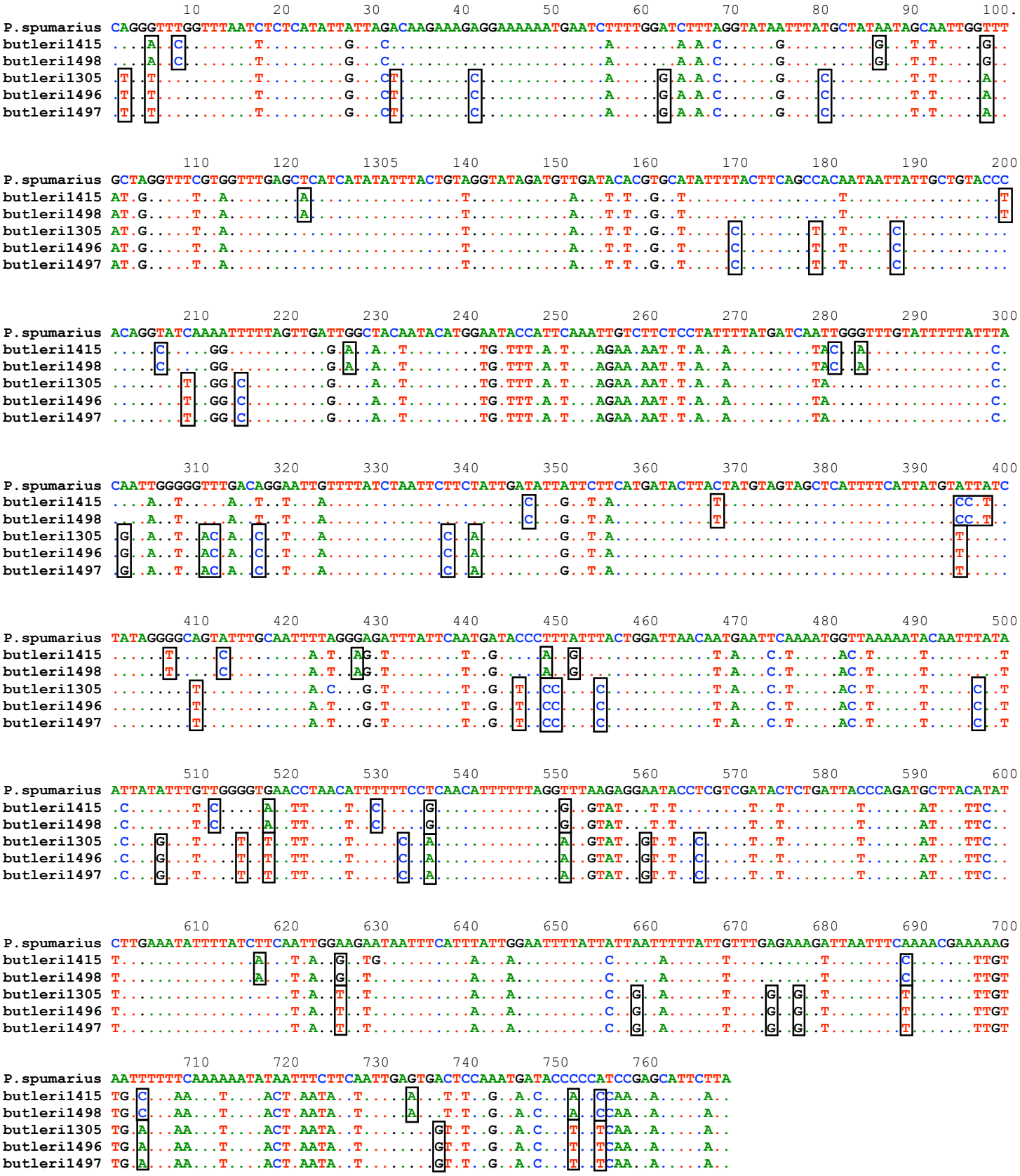

Figure 14. COI sequences of *Kybos butleri*, positions of the two different genotypes are marked with squares. Numbers indicate base pair positions.

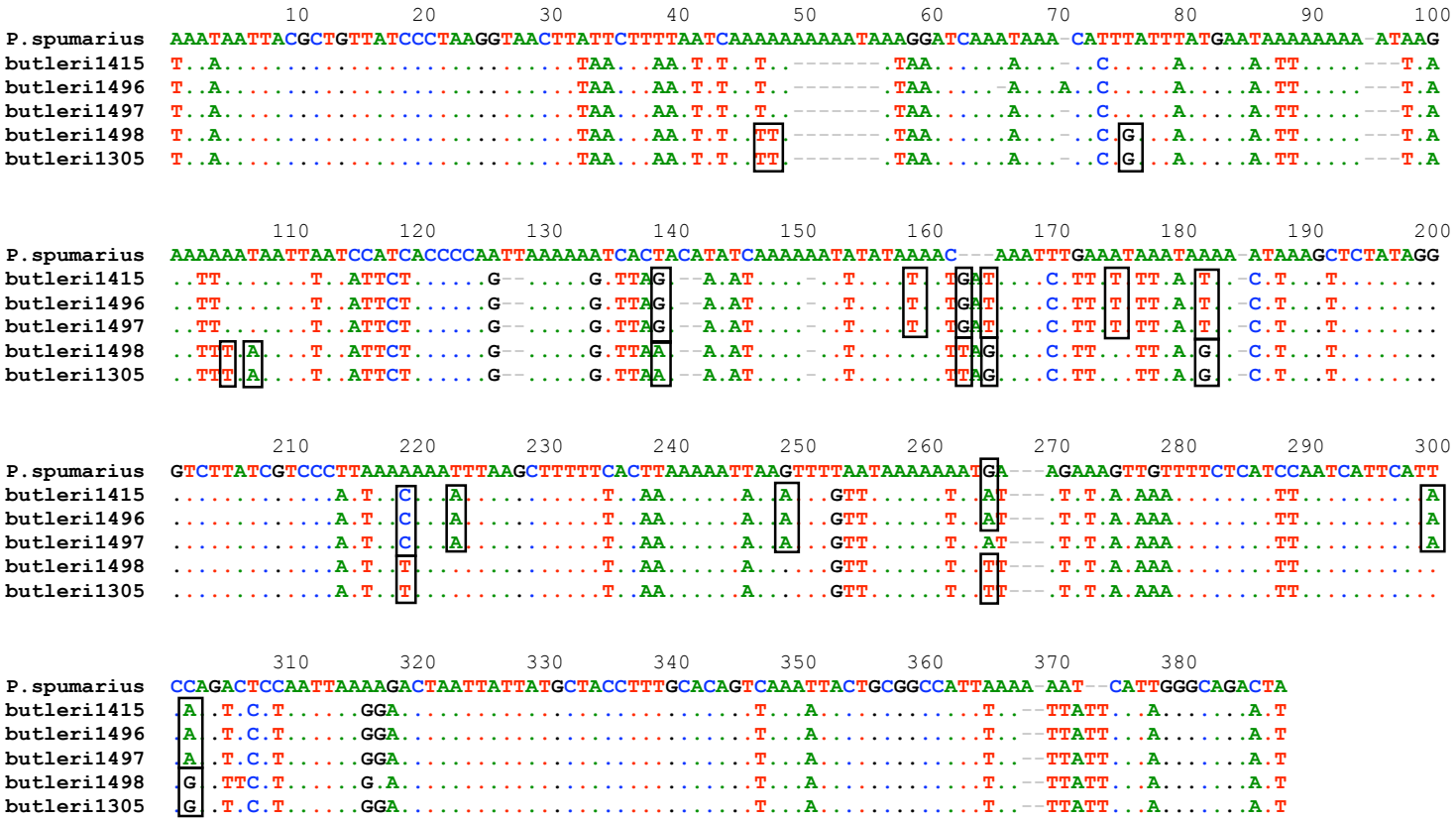

Figure 15. 16S sequences of *Kybos butleri*, positions of the two genotypes are marked with squares. Numbers indicate base pair positions.

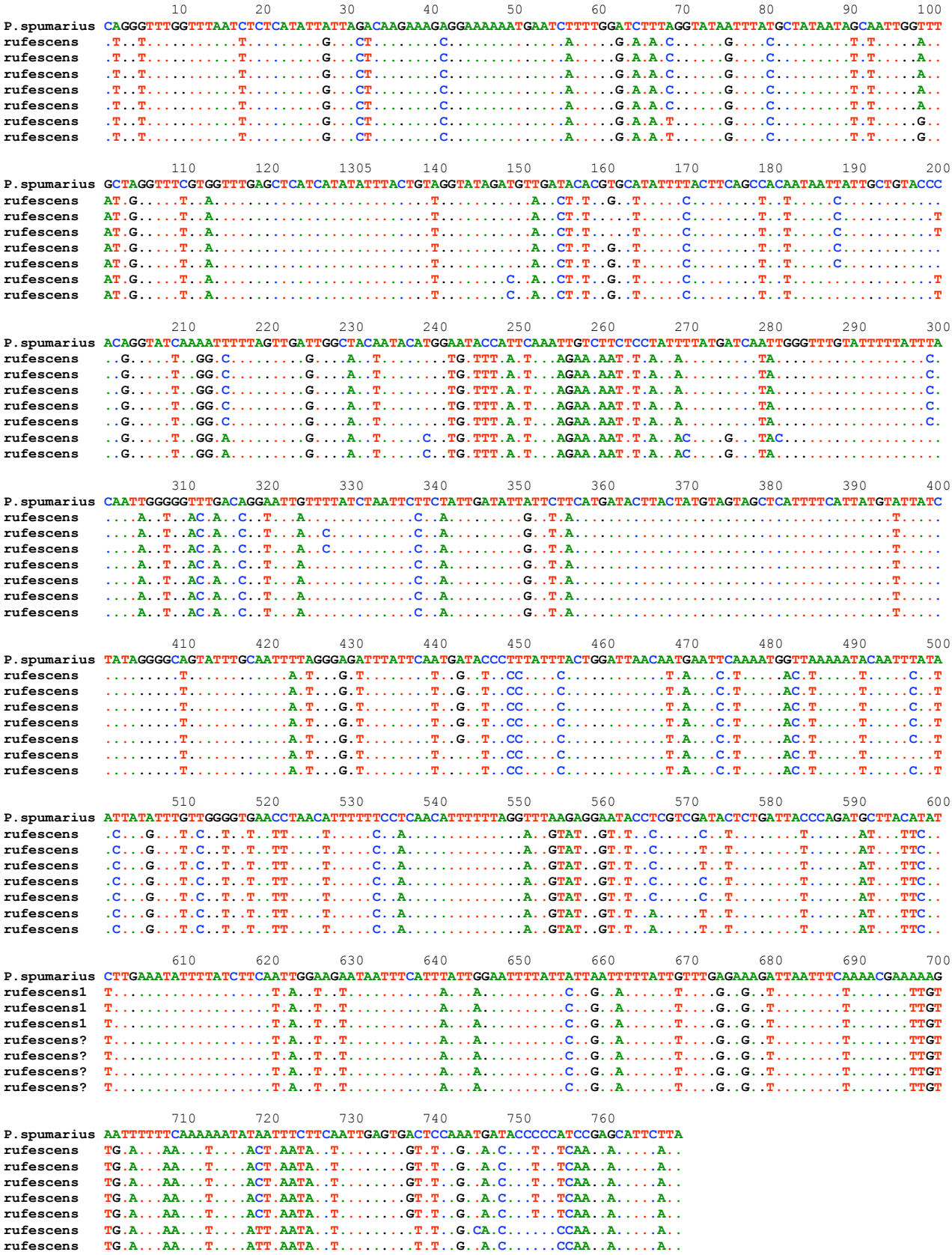

Figure 16. COI sequences of all examined *Kybos rufescens* individuals. Numbers indicate base pair positions.

3.1.6 Bioacoustics

We recorded male songs of the following species: *Kybos rufescens*, *K. strobli* and *K. lindbergi.* Unpublished songs of *Empoasca* s.str. were available from other studies made by the research group in Ljubljana (M. Virant-Doberlet, pers. comm.). Males were calling all the time whereas females responded only if they were virgins. Already mated females did not reply to the male calling songs.

The sonograms (Fig. 17) show the time pattern of the calls as well as the frequency range (spectrograms). The common male calling song of *K. lindbergi* has a main frequency of about 0.3 kHz which rises to around 1.0-1.5 kHz at the end of the bursts. The song consists of usually three short bursts, each not longer 1 s. The starting burst is always longer than the following ones. *K. strobli* possesses a monotonic call of about 5-6 s. At the beginning the frequency is low (0.2 kHz) and increases up to 2.0-2.5 kHz. In the sonogram of *K. rufescens* we see both, the common male calling song and the female response. The male song consists of two strong bursts with a main frequeny of 2.0 kHz and a second somewhat weaker burst at 3.6 kHz. Each burst lasts just under 1 s. The female response is extremely weak and of low frequency (around 0.1 kHz). Also the time of the bursts are very short (0.1-0.25 s). Two of the female bursts are only visible on the spectrogram because they are simultaneous with the male calls. The sonogram depicts only a portion of a longer duet between the sexes.

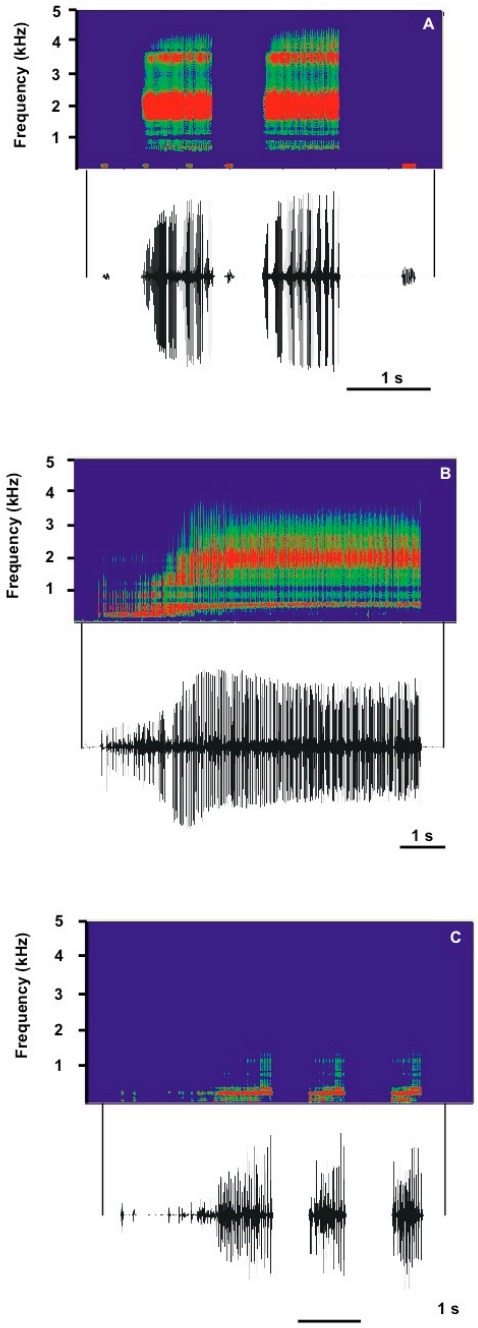

Figure 17. A-C, sono- and spectograms of the common male calling song of Kybos spp. A, K.rufescens; B, K. strobli, C, K. lindbergi.

3.2 Phylogeny

3.2.1 Morphological analysis

A cladistic analysis was performed with 21 taxa (*Kyboasca* 1 species, *Empoasca* 1 species, *Kybos* 19 species) using 16 characters (Tables 1-2). Three characters relate to the wings, 6 to the aedeagus, 1 to the anal collar, 5 to the female genitalia and 1 to the nymph. All characters are binary except for characters 6, 10 and 15 which are multistate. A heuristic analysis was performed using NoNa (Goloboff, 2001), WinClada (Nixon, 2002) and PAUP*4.10 (Swofford, 1998). The analysis resulted in 48 most parsimonious trees with following parameters: length = 43, consistency index = 62, retention index = 80.

Fig. 18 shows the consensus tree (nelsen) with a strongly supported monophyletic *Kybos* (arrow). Within *Kybos* the general resolution is relatively weak. There are 6 groups: group 2 is strongly supported and includes the taxa with aedeagal appendages. Groups 1, 3 and 4 are weakly supported by a single synapomorphy each and groups 5 and 6 are supported only by homoplasies. Group 4 contains all the taxa associated with Betulaceae.

Of the 16 characters used in the analysis nine constitute synapomorphies (Fig. 18, dark circles). Four of the synapomorphies refer to female characters, three to wing characters and only two to aedeagal characters.

Table 1. Morphological characters used for cladistic analysis (Table 2, Fig. 18).

1. Second apical cell in fore wing stalked (0); not stalked (1);
2. Commisural border of fore wing concolorous (0); bearing a brown band (1);
3. Colour of corioclaval suture of fore wing black or fuscous (0); concolorous with forewing (1);
4. Aedeagus without appedages (0); with appendages (1);
5. Aedeagus with divergent appedages (0); with parallel sited appedages (1);
6. Appedages of aedeagus (in lateral view) parallel to main stem (0); dorsaly of main stem (1); ventraly of main stem (2);
7. Length of aedeagal appedages as long as stem (0); shorter than stem (1);
8. Basis of aedeagal appedages widely apart from each other (0); close to each other (1);
9. Aedeagal appedages apically pointed (0); blunt (1);
10. Process of anal collar very short and pointed (0); long and slender (1); short and stout (2);
11. Female sternit 7 with a prolongated lobe (0); without a prolongated lobe (1);
12. Ventral edge of median valvula apically evenly curved (0); apically strongly curved (1);
13. Structure of teeth of valvula regularly triangular (0); irregularly blunt (1);
14. Base of first valvifer with a median ridge (0); without a median ridge (1);
15. Distal edge of base of first valvifer straight (0); rounded 'hook-shaped' (2);
16. Length of larval tibia 3 about half of the body length (0); less than half of the body length (1).

Table 2. Matrix of the morphological characters used for the cladistic analysis (Fig. 18). For characters see Table 1.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
bipunctata	1	0	1	0	-	-	-	-	-	0	1	0	0	1	0	?
vitis	1	0	1	0	-	-	-	-	-	1	1	0	0	1	1	?
abstrusus	0	0	1	0	-	-	-	-	-	1	0	0	1	1	2	?
aetnicola	0	0	0	1	0	2	0	1	0	2	0	1	1	0	0	0
austriacus	0	0	0	1	1	0	0	1	0	2	0	1	1	0	0	?
butleri	0	1	1	0	-	-	-	-	-	1	0	0	1	1	2	?
calyculus	0	0	0	1	0	2	1	1	0	2	0	1	1	0	0	?
candelabricus	0	0	0	1	0	0	0	0	0	2	0	0	1	0	1	?
digitatus	0	0	0	1	1	1	1	0	1	1	0	0	1	0	1	?
limpidus	0	0	1	0	-	-	-	-	-	1	0	0	1	1	2	1
lindbergi	0	0	0	1	1	0	1	1	0	2	0	1	1	0	0	0
ludus	0	0	0	1	1	0	1	0	0	2	0	1	1	0	0	0
mesasiaticus	0	0	1	0	-	-	-	-	-	1	0	0	1	1	2	?
mucronatus	0	0	0	1	0	2	1	1	1	2	0	0	1	0	0	?
populi	0	0	1	0	-	-	-	-	-	1	1	0	1	1	2	1
rufescens	0	1	1	0	-	-	-	-	-	1	0	0	1	1	2	?
smaragdula	0	0	0	1	1	1,2	1	0	0	2	0	1	0	0	0	1
sordidulus	0	0	1	0	-	-	-	-	-	1	1	0	1	1	2	?
strigilifer	0	0	0	1	0	0	1	1	0	2	0	1	1	0	1	?
strobli	0	0	0	1	0	1	1	1	0	2	0	1	0	0	0	?
virgator	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	?

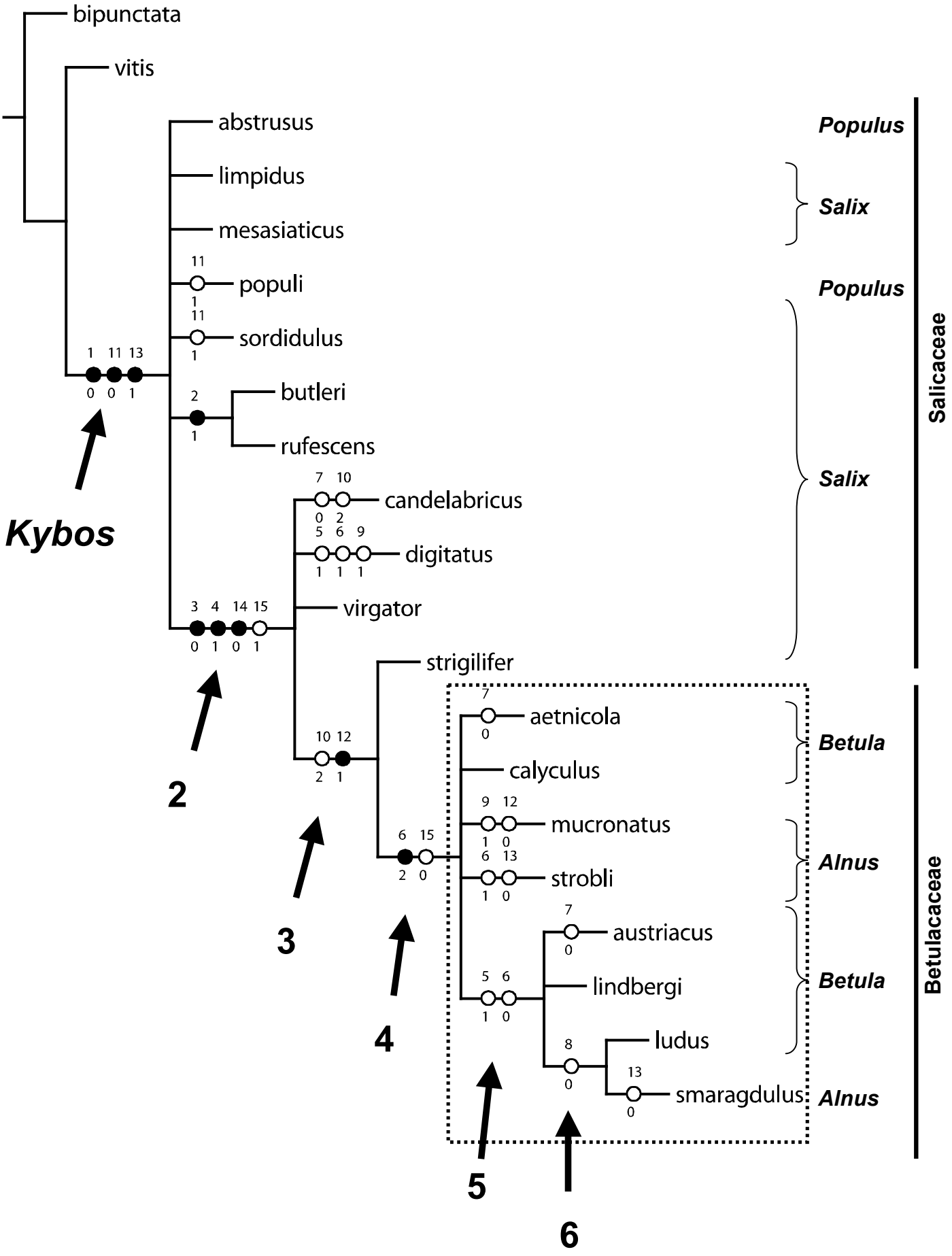

Figure 18. Cladogram based on morphological characters compared to host plant information

3.2.2 Molecular analyses

Within *Kybos* species 479 of the 769 bp of COI are constant and 178 characters are parsimony-informative. Gaps were treated as "missing" characters. The resulting tree has the following parameters: length = 548, consistency index = 0.6971, retention index = 0.8061, homoplasy index = 0.3029. In the 16S sequences 226 of the 382 characters are constant, 72 bp are parsimony-informative. Gaps were treated as "missing" characters. The obtained tree has following parameters: lenght = 245, consistency index = 0.841, retention index = 0.843, homoplasy index = 0.159.

Fig. 19 shows the tree obtained from COI, fig. 20 the resulting tree from 16S. The tree from COI is better resolved than the one from 16S. *Kybos* forms in both trees a monophyletic group. In the COI we can recognize following well supported groups: *calyculus*, *digitatus*, *lindbergi*/*ludus*, *smaragdula* and the Central Asiatic group including *dentifera*, *mesasiaticus*, *soosi*. *K. butleri* is polyphyletic and appears at two different places and does not consist of the same groupings in COI and 16S.

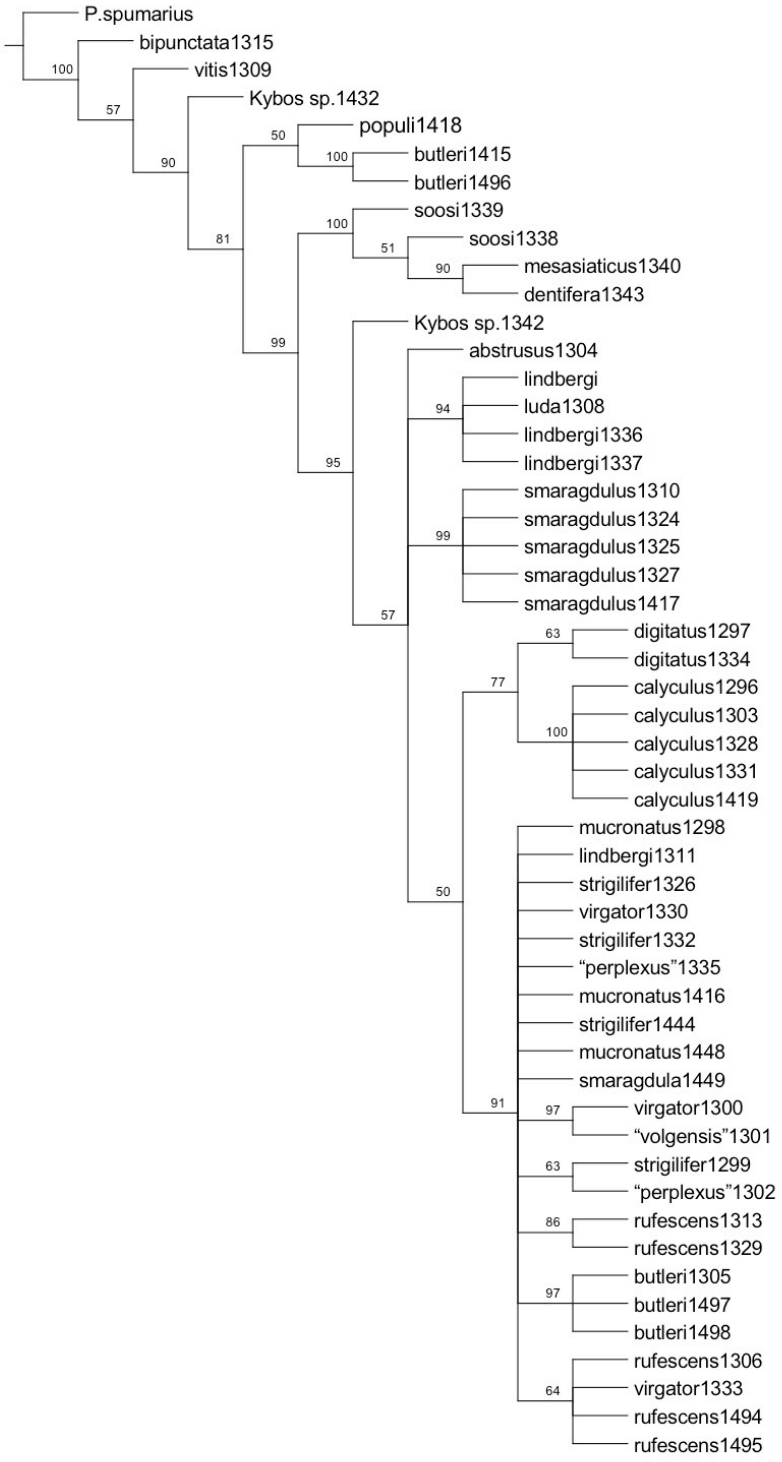

Figure 19. Consensus tree obtained from COI sequences. Numbers on branches indicate bootstrap values.

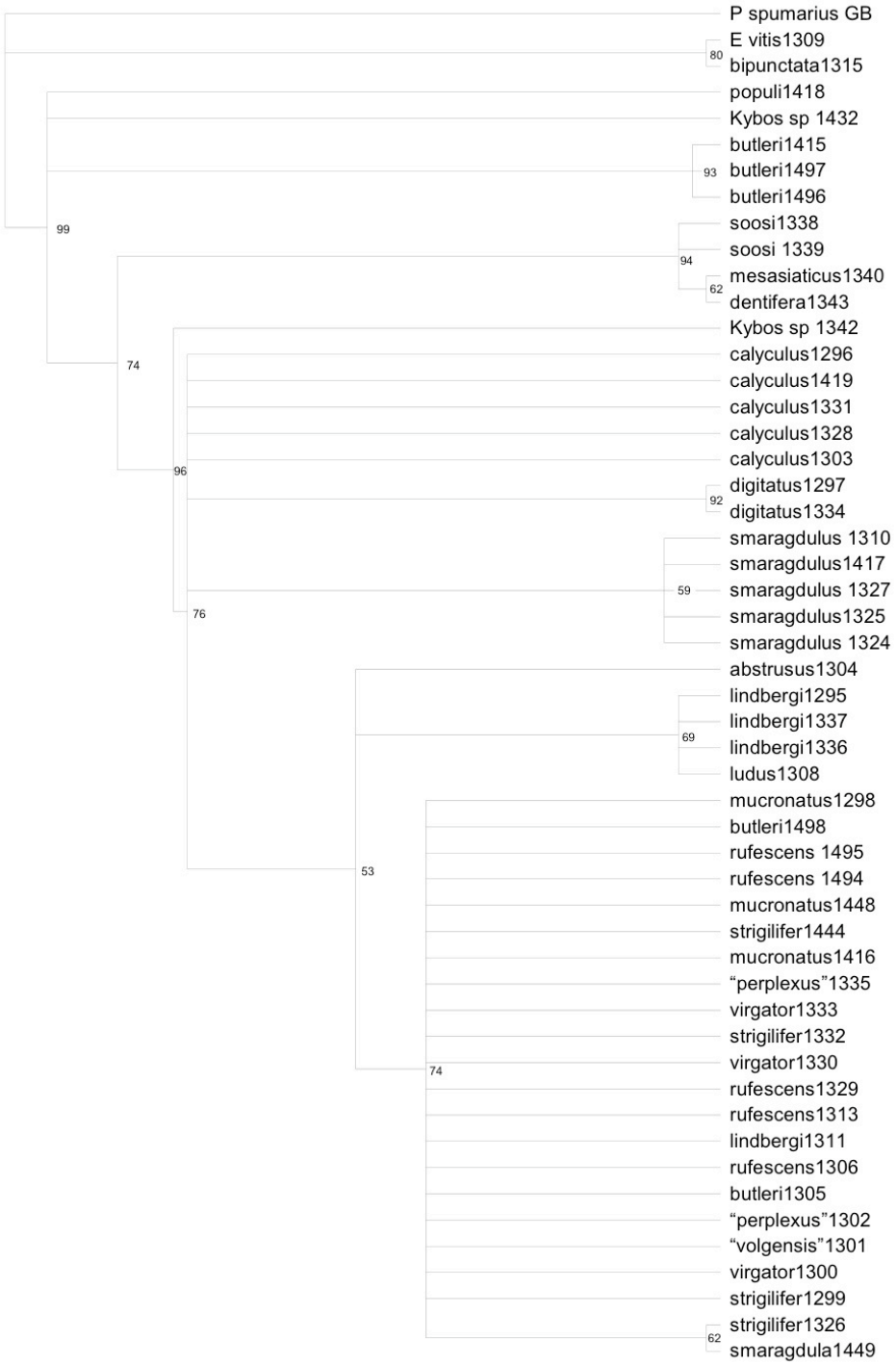

Figure 20. Consensus tree obtained from 16S sequences. Numbers on branches indicate bootstrap values.

3.3 Distribution and host associations

Most Central European *Kybos* species are widely distributed and occur in high abundance where their host plants grow. They generally occur also on a wide altidudinal range (e.g. *K. rufescens* and *K. lindbergi* in Switzerland from Basel at 280 m and Bever at 1700 m). Only a few species are restricted. *K. aetnicola* is endemic to higher elevations of Mt. Etna, Sicily, *K. austriacus* occurs in higher elevations the Austrian and Swiss Alps but is always very rare. Also *K. strobli* is restricted to higher elevations in the Alps but has a wider distribution and is relatively common.

K. ludus and *K. lindbergi* form in Europe a vicariant species pair: *K. ludus* in the West and Southwest, as well as *K. lindbergi* in the East and Northeast respectively (Fig. 21). The two species occur together in a small area in Germany and Switzerland where morphological intermediates can be found relatively frequently. This area is a possible hybrid zone.

Unlike most Central European species *K. calyculus* and *K. digitatus* are only rarely collected and little is know about their biology.

All species outside Europe and most European species are associated with *Salix* and *Populus* species. Some European species are associated with *Alnus* or *Betula* spp. Detailed information on host ranges is lacking for most species. From the available field data it appears that species are restricted to a single host genus where they are narrowly oligophagous on a few closely related species. Only a few species are monophagous on a single host species: *K. digitatus* on *S. elaeagnos*, *K. rufescens* on *S. purpurea*, *K. abstrusus* on *P. nigra*, *K. aetnicola* on *B. aetnensis*. For some species confirmed host information is scarce (*Kybos mucronatus* only on *A. glutinosa* and *K. strobli* on *A. incana*?).

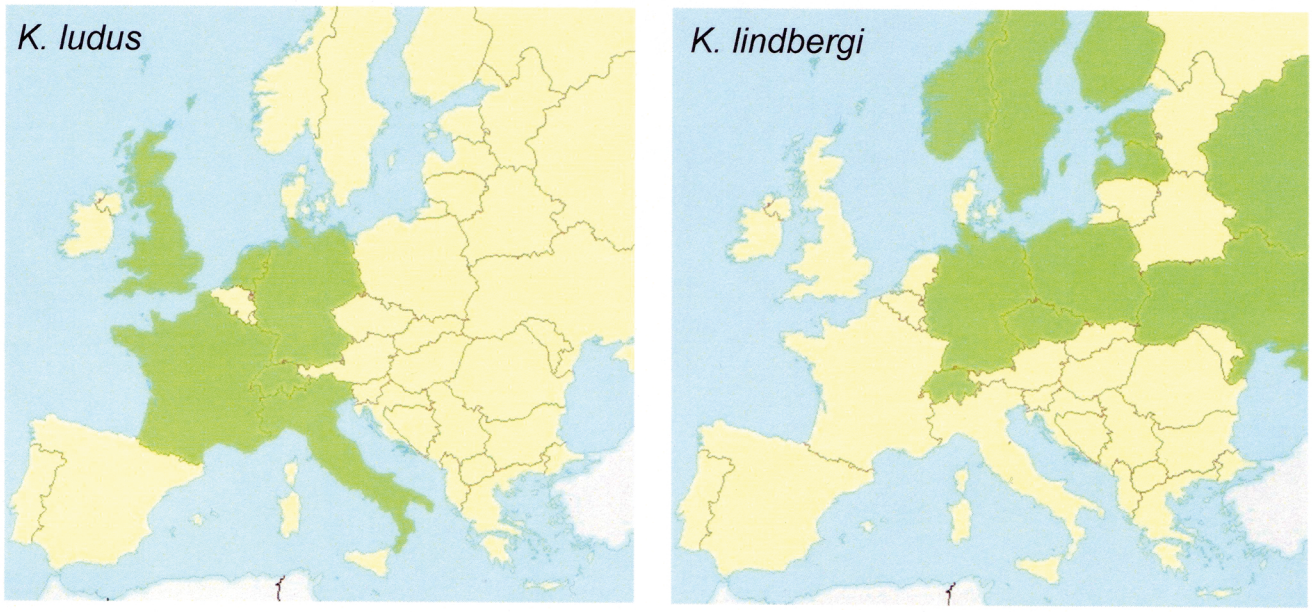

Figure 21. Distribution of *Kybos ludus* and *K. lindbergi* in Europe (after Fauna Europaea, revised).

4 Discussion

4.1 Taxonomy

As in many other cicadellid genera, the morphological differences between *Kybos* species are generally small. Species are mostly diagnosed by the aedeagus and the apodemes, both structures of the male. Additional diagnostic characters previously used are the anal collar and pygofer of the male, fore wing pattern and colour, sternite VII of female and host plant association. This leads to the unsatisfactory situation that in many cases females and nymphs cannot be identified and that identifiation without host information can be tricky. In addition there is the problem with the apodemes, that they reach their final extension only a few days after the final adult moult. Günthart (1977) documented this variation in other typhlocybine taxa (several *Flammigeroidia* species, *Empoasca decipiens* and *Eupteryx melissae*). The aedeagal shape is considered to be a good species diagnoser but there are not enough studies investigating the intraspecific variability of this character. In fact, this may be one of the reasons why currently also the identification of some males can be difficult. At the current state it seems probable that some nominal species have been described on the basis of teneral males with undeveloped apodemes, and others on too narrowly interpreted aedeagal variations. We expected that a thorough revision of *Kybos* species using morphology would reduce the number of currently recognised Central European species. We also expected that additional diagnostic characters in females and nymphs may be found.

Despite detailed investigations our study did not yield additional morphological characters in the males for species diagnosis but we confirm that the two structures (aedeagus and apodemes) are, in principal, the major species diagnosers.

Our assumption that previously teneral specimens with undeveloped apodemes were decribed as distinct nominal species was confirmed in the following example. *K. volgensis* differs from *K. virgator* only in the shorter apodemes as well as some minor differences in the shape of the aedeagus. The difference of the aedeagal appendages does not exceed the variablilty found within a single population of *K. virgator*. Here we suggest that *K. volgensis* is a junior synonym of *K. virgator.* Depending on the collecting date a large number of immature adults can be found which may lead to the erroneous conclusion that the shape of the appodemes is fully developed. This suggestion can be easily veryfied by additional sampling at the same site a few days later.

The problem of intraspecific aedeagal variation is more difficult to resolve. It is necessary to examine a large number of specimens and carry out breeding experiments. Such breeding experiments were made by Günthart (1974). She showed that the variation of the

aedeagus within *K. strigilifer* is marked but she did not draw any taxonomic conclusions. The present study documents that the characters diagnosing *K. perplexus* (and *paraltaicus*) fall within the variation encountered in *K. strigilifer*. *K. perplexus* is therefore synonymised with *K. strigilifer*. Looking outside the Central European fauna the large number of species known from a few specimens only is striking. Our hypothesis is that a number of these taxa will turn out to be synonyms of other taxa.

Other characters such as the wing coloration and the anal collar and pygofer of males bear only limited taxonomic information on species level. They are mostly useful to define species groups. We observed more or less the same with the female genitalia. Here the most important diagnostic character is the shape of the ovipositor base. With a few exceptions (*K. butleri*, *K. populi*) it is not possible to diagnose species with female sexual characters. Nymphal characters are even less informative.

The bioacoustic studies suggest that the songs are highly diagnostic. Probably one of the main purposes of these calls is to attract and find mates. With this hypothesis we would expect that closely related sympatric species differ strongly in their songs. The sound is produced by the so called apodemes. These are specialised internal, often striated areas of cuticle located at the two or three basal abdominal tergites and sternites respectively. Differences in the shape of the apodemes are responsible for different sounds (but not necessarily vice versa). The songs of the three recorded species are drastically different but more species should be examined. Comparing *Kybos* songs with songs of representatives of *Empoasca* s.str. show that there are significant differences in frequency modulation.

Regarding the molecular data we observed that the COI sequences are more informative than those from 16S mtDNA. But the "barcoding gene" COI is only partially informative within the genus *Kybos* with respect to species diagnosis. Some species such as *K. calyculus* and *K. digitatus* are homogenous, many others, however, are quite variable. Remarkable are the two haplotypes of *K. butleri.* They are not related to geographically separated populations because specimens from a particular locality represented a mixture of both haplotypes. Failure of COI to diagnose species was also found in other groups (Sperling 2003; Meier *et al.* 2006).

Kybos is well-characterised by the wing venation, male and female genital structures. Here we add bioacoustic and molecular support for its monophyly. *Kybos* has been treated as genus (mostly by European workers) or as subgenus of *Empoasca* (mostly North American authors). Here we follow the European tradition. *Empoasca*, on the other hand, is in its current state probably paraphyletic.

4.2 Phylogeny

Both the morphological and molecular trees are poorly resolved. But in all trees *Kybos* forms a monophyletic group. In the cladistic analysis based on morphology the female genital structures and wing characters are the most informative ones. Male characters are, in contrast to the taxonomy, much less important for the tree structure. Six groups are recognised of which only one is strongly supported (Fig. 18). Group 2 includes all species which bear aedeagal appendages. The other groups are weakly supported. Interesting is the fact, that group 4 consists of all taxa living on Betulaceae. Our groups are similar to the groups established by Dworakowska (1976) but less resolved. Dworakowska proposed the following groupings based on morphology and host plant information (the species examined here are in bold):

smaragdula-group: ***aetnicola***, ***austriacus***, ***calyculus*****,** ***digitatus***, ***lindbergi***, ***ludus***, ***smaragdulus*** and ***strobli***
mucronatus-group: *auricillatus*, ***candelabricus***, ***mucronatus*** (incl. *mucronatus verbae*), ***strigilifer*** (incl. *perplexus*) and ***virgator*** (incl. *volgensis*)
limpidus-group: *cornutus*, *dlabolai* and ***limpidus***
butleri-group: ***abstrusus***, ***butleri***, *chadchalicus*, *iliensis*, *koreana*, ***mesasiaticus***, *mitjaevi*, *niveicolor niveicolor*, *niveicolor japonicus*, ***populi***, *pyramidialis*, *rubrovenosus*, ***rufescens*** (incl. *rufescens rufescens* and *rufescens matsumurai*), *soosi* and possibly *oshanini*
sordidulus belongs to the Nearctic *trifasciatus*-group (established by Ross, 1963)

The topologies of the two molecular cladograms (Figs. 19-20) are similar but with significant differences (e.g. grouping of *K. butleri*). The 16S tree is less resolved than that of COI. Apart from the monophyly of *Kybos* there is no congruence between the morphological and molecular trees. All trees show, that *Kybos* is monophyletic.

We think that the phylogeny obtained from morphological characters is more reliable than the molecular phylogeny. The cladistic analysis based on morphology uses different character systems (wing coloration, male genitalia, female genitalia and nymphal characters). The congruence of these different character systems provides a more stable hypothesis than the trees obtained from molecular data. Predictions are only possible for the morphology, but not for the COI and 16S sequences.

4.3 Biogeography

Both *Kybos* and *Kyboasca* are restricted to the Holarctic Region whereas *Empoasca*, in its present probably paraphyletic definition, has a world-wide distribution. Of the 114 currently known *Kybos* species (Appendix 4), 42 are restricted to the Palaearctic, 76 to the

Nearctic and only 4 occur in both regions (*K. butleri*, *K. ludus*, *K. smaragdulus* and *K. sordidulus*). The first three have almost certainly been introduced from the West Palaearctic into the Nearctic. Introductions are documented also for other biogeographic regions. *K. lindbergi*, *K. ludus* and *K. smaragdulus* have been introduced with their host plants into Australia and New Zealand (Dumbleton 1964; Knight 1976; Fletcher & Knight 1998). *K. sordidulus* may be genuinely Holarctic though further research is needed. More species are currently known from the western part of the Nearctic than from the eastern part. As the available information on Nearctic species is scarce it is not possible to decide whether this pattern is real or just an artifact. A similar situation is found in the Palaearctic Region. The knowledge on the West Palaearctic *Kybos* fauna is much more complete than that of the East Palaearctic Region.

In Europe most species are widely distributed but two species are restricted to higher elevations in the Alps (*K. austriacus*, *K. strobli*) and *K. aetnicola* has been recorded only from Sicily. Incidentally the three species belong to the highly derived clade of Betulaceae feeders but they do not form a monophyletic group.

According to Asche & Hoch (2004) (Fig. 21) *K. ludus* occurs mainly in Western Europe, whereas *K. lindbergi* lives in Northern and Eastern Europe. Both species feed on *Betula* and differ only in subtle details of the aedeagus. In Germany and Switzerland both species are sympatric and intermediate forms are frequent. This hybrid zone was already mentioned by Dworakowska (1976). Although our investigations based on morphology and molecular techniques did not clarify the problem of these two closely related species, we suggest to treat the two taxa as distinct species which are geographically separated. Only in a relatively small area in Central Europe we can find hybrids between *K. lindbergi* and *K. ludus*.

4.4 Host plants

Species of *Kybos* and of its presumed sister group *Kyboasca* are generally monophagous on various genera of woody Dicotyledones, the former on Salicaceae and Betulaceae (Appendix 4), the latter on Fabaceae, Rosaceae, Ulmaceae etc. Species of *Empoasca* s.str., in contrast, are polyphagous on a variety of herbaceous and woody dicotyledonous families.

Apart from three West Nearctic species (*K. cascada*, *K. fontana* and *K. incida*) which have been reported from both *Populus* and *Salix* spp. all members of *Kybos* are restricted to a single host genus. The species associated with a particular genus, however, do not form a monophyletic group. Most *Kybos* spp. are associated with Salicaceae except for nine West Palaearctic species which live on Betulaceae (six on *Betula*, three on *Alnus*). It is interesting

to note that the Betulaceae feeders form a monophyletic group in the morphological cladistic analysis (Fig. 18) suggesting a single host shift from Salicaceae to Betulaceae. This host shift happened only in the West Palaearctic.

5 Conclusions

The taxonomy of *Kybos* was traditionally based mostly on the morphology of the male genitalia, in particular the aedeagus and the apodemes. Our study on the Central European members confirms that these characters are the prime diagnostic structures. However, intraspecific variation of the aedagus has previously not been sufficiently examined, a notable exception beeing the work of Günthart (1974). In some cases individuals with morphological extremes have been attributed to independent species creating taxonomic chaos, e.g. *K. perplexus* as morphological extreme of *K. strigilifer*. Some caution is also required with respect to the apodemes which are only fully developed a few days after eclosion. In the past the apodemes of teneral males have been misjudged and provided the base for the erection of species, e.g. *K. volgensis* as teneral form of *K. virgator*. Other male genital characters such as the pygofer, the stylus and the anal collar, as well as wing coloration, can be used for separating species groups but are not diagnostic at species level. Unfortunately this is also true for the female genitalia and even more so for nymphal characters. We expect that a similar situation can be found in other genera of Typhlocybinae.

As with morphology alone many individuals (mostly females) cannot be identified other character systems are required. Molecular methods have been successfully applied to this sort of problem, in particular sequence data of the genes COI, 16S, wingless, NADH, 18S and others. Good results with this method led to the idea that a single gene fragment may suffice to diagnose each organismal species. This approach, known as “barcoding of life” uses the COI gene (Hebert *et al*. 2003; Tautz *et al*. 2003). After initial euphoria several papers have been published recently demonstrating that COI shows at least in some species considerable variation (Sperling 2003; Hickerson *et al*. 2006; Meyer *et al.* 2006). Our study confirms these observations and adds some more examples to the list of morphologically well-defined species which are supported neither by COI nor 16S, e.g. *K. butleri* and *K. rufescens*. The taxonomic situation within *Kybos* remains unaltered despite our molecular study, i.e. females can often not be attributed to a species with certainty.

As for the taxonomy neither the morphological nor the molecular cladistic analyses provided sufficient information for constructing a fully resolved phylogeny of *Kybos*. Both approaches support its monophyly but otherwise the results from these data sets are quite different. The morphological tree is better supported and is congruent, to a certain extent, with host plant associations. In the absence of a fully resolved tree it is impossible to investigate detailed evolutionary patterns in the diversification of the genus *Kybos*, i.e. the contribution of coevolution with the hosts or host shifts versus geographical vicariance or dispersal as forces

for speciation. It is generally assumed that coevolution is the major force but studies have shown that geographic vicariance is more important at least in some groups (Burckhardt & Basset 2000; Percy 2003; Burckhardt & Ouvrard 2007). In *Kybos* there are no detectable patterns of coevolution or biogeographic vicariance but there is a monophyletic group, restricted to the West Palaearctic, associated with Betulaceae (contrasting the remainder of species on Salicaceae). While most species are widely distributed a few are endemic to small areas at higher elevations (Alps, Mt. Etna).

For resolving the remaining taxonomic problems of Central European *Kybos* species, in particular closely related sympatric taxa, breeding experiments and additional bioacoustic studies are requirered. For a better resolution of the phylogeny additional taxa, including Nearctic species, should be added and sequences of other genes should be investigated. Additional targeted field work should provide further details on the distribution of individual *Kybos* species as well as host associations.

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Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos abstrusus	1♂	Bulgaria	19.07.1971	P. Lauterer	MZMB	
Kybos abstrusus	1♂	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	
Kybos abstrusus	1♀	Finland, Turku	28.08.1948	R. Linnavuori	AMNH	
Kybos abstrusus	1♂	France, Strasbourg	13.09.1993	I. Malenovský	MZMB	
Kybos abstrusus	1♂	Slovakia, Palúzdka	15.07.1963	P. Lauterer	MZMB	
Kybos abstrusus	9♂ 5♀	Slovakia, Palúdzká	15.07.1963	P. Lauterer	MZMB	
Kybos abstrusus	8♂ 5♀	Slovakia, Palúdzká	15.07.1963	P. Lauterer	MZMB	
Kybos abstrusus	1♂	Slovakia, Oslany	10.07.1977	P. Lauterer	MZMB	
Kybos aetnicola	2♂ 6♀ 1 nymph	Italy, Mt. Etna	30.08.1948	Hartig	INER	type series
Kybos austriacus	1♂	Slovakia, Betliar	11.07.1979	P. Lauterer	MZMB	
Kybos austriacus	1♂	Switzerland, Zernez	26.08.1977	H. Günthart	Coll. Günthart	
Kybos austriacus	1♂	Switzerland, Mte. Brè	03.08.1983	L. Rezbanyai	NHMB	
Kybos austriacus	1♂	Switzerland, Zernez	18.08.1987	H. Günthart	Coll. Günthart	
Kybos austriacus	2♂	Switzerland, Zernez	21.08.1987	H. Günthart	Coll. Günthart	
Kybos austriacus	1♀	Switzerland, Zernez	21.08.1987	H. Günthart	Coll. Günthart	
Kybos butleri	3♂ 5♀	Austria, Oberrakitsch	21.09.1996	P. Lauterer	MZMB	
Kybos butleri	1♂	Bulgaria	20.07.1971	P. Lauterer	MZMB	
Kybos butleri	1♂	Bulgaria	27.07.1972	P. Lauterer	MZMB	
Kybos butleri	1♂	Czech Republic, Sakvice	27.08.1973	P. Lauterer	MZMB	
Kybos butleri	5♂	Czech Republic, Moravia mer.	19.06.1980	P. Lauterer	MZMB	
Kybos butleri	1♂	Czech Republic, Chriby	21.08.1980	P. Lauterer	MZMB	
Kybos butleri	1♂	Czech Republic, Moravia centr.	21.08.1980	P. Lauterer	MZMB	
Kybos butleri	3♂	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	
Kybos butleri	2♂ 1♀	Czech Republic, Bilé Karpaty	09.09.1998	I. Malenovský	MZMB	
Kybos butleri	3♀	Czech Republic, Bilé Karpaty	09.09.2000	I. Malenovský	MZMB	
Kybos butleri	1♂	Germany, Weil am Rhein	27.07.2000	R. Mühlethaler	NHMB	
Kybos butleri	1♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	
Kybos butleri	1♂	Switzerland, Basel	22.06.2000	R. Mühlethaler	NHMB	
Kybos calyculus	1♂	Czech Republic, Charvatská	31.07.1974	P. Lauterer	MZMB	
Kybos calyculus	3♂	Czech Republic, Brno-Slatina	21.06.2003	R. Mühlethaler	NHMB	
Kybos candelabricus	2♂ 3♀	Turkey, Topasulag	16.06.1970	J. Dlabola	NMP	
Kybos candelabricus	1♂ 5♀	Turkey, Ankara	08.-10.8.1963	R. Linnavuori	NMP	
Kybos digitatus	2♂	France, Rougon	26.08.1996	I. Malenovský	MZMB	
Kybos digitatus	1♂	Germany, Weil am Rhein	27.07.2000	R. Mühlethaler	NHMB	
Kybos digitatus	1♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	
Kybos digitatus	9♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos digitatus	1♀	Germany, Weil am Rhein	19.08.2002	R. Mühlethaler	NHMB	
Kybos digitatus	1♀	Germany, Weil am Rhein	11.06.2003	R. Mühlethaler	NHMB	
Kybos digitatus	2♀	Germany, Weil am Rhein	23.07.2004	R. Mühlethaler	NHMB	
Kybos digitatus	5♂ 3♀	Germany, Weil am Rhein	29.07.2004	R. Mühlethaler	NHMB	
Kybos digitatus	1♂	Switzerland, Basel	19.08.2001	R. Mühlethaler	NHMB	
Kybos limpidus	1♂	Bulgaria	27.07.1972	P. Lauterer	MZMB	
Kybos limpidus	1♂ 3♀	Czech Republic, Sakvice	27.08.1973	P. Lauterer	MZMB	
Kybos limpidus	3♂ 4♀	Germany, Berlin-Hermsdorf	10.08.2002	R. Mühlethaler	NHMB	
Kybos limpidus	4 nymphs	Poland, Warsaw	24.08.1973	I. Dworakowska	AMNH	
Kybos limpidus	1♀	Poland, Warsaw	29.08.1973	I. Dworakowska	Coll. Günthart	
Kybos limpidus	2♂ 5♀	Poland, Warsaw	29.08.1973	I. Dworakowska	AMNH	
Kybos lindbergi	1♂	Bulgaria	27.07.1972	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Brno-Staró	20.09.1965	P. Lauterer	MZMB	
Kybos lindbergi	5♂	Czech Republic, Jeseník-Vel.	20.09.1970	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Moravia mer.	14.08.1975	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Moravia occ.	16.06.1977	P. Lauterer	MZMB	
Kybos lindbergi	3♂ 4♀	Czech Republic, Moravia occ.	05.09.1978	P. Lauterer	MZMB	
Kybos lindbergi	3♀	Czech Republic, Ridelov	05.09.1978	P. Lauterer	MZMB	
Kybos lindbergi	4♂ 8♀	Czech Republic, Moravia mer.	13.09.1978	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Moravia occ.	30.08.1979	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Moravia occ.	30.08.1979	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Czech Republic, Moravia centr.	17.06.1981	P. Lauterer	MZMB	
Kybos lindbergi	5♂	Czech Republic, Moravia or.	24.06.1982	P. Lauterer	MZMB	
Kybos lindbergi	2♂ 2♀	Czech Republic, Brno-Mokrá	18.06.1994	P. Lauterer	MZMB	
Kybos lindbergi	8♀ 1 nymph	Czech Republic, Hodonín-Pánsv	17.08.1995	P. Lauterer	MZMB	
Kybos lindbergi	3♀	Czech Republic, Bilé Karpaty	14.09.1999	I. Malenovský	MZMB	
Kybos lindbergi	20♂	Czech Republic, Brno-Slatina	21.06.2003	R. Mühlethaler	NHMB	
Kybos lindbergi	2♂ 1♀	Finland, Turku	07.07.1974	H. Günthart	Coll. Günthart	
Kybos lindbergi	1♂ 1♀	Poland, Kosobudy	12.07.1966	I. Dworakowska	AMNH	
Kybos lindbergi	5♂ 15♀	Slovakia	11.07.1979	P. Lauterer	MZMB	
Kybos lindbergi	1♂	Switzerland, Riehen	26.05.2000	D. Wyniger	NHMB	
Kybos lindbergi	1♂	Switzerland, Dielsdorf	19.07.2002	R. Mühlethaler	NHMB	
Kybos lindbergi	1♂	Switzerland, Basel	20.07.2002	R. Mühlethaler	NHMB	
Kybos ludus	1♂	USA, Wooster, Ohio	1917	D.M. DeLong	OSU	holotype
Kybos ludus	1♂	Bulgaria	27.07.1972	P. Lauterer	MZMB	
Kybos ludus	2♂	Switzerland, Uster	25.07.1977	H. Günthart	Coll. Günthart	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos ludus	1♂	Switzerland, Zernez	26.08.1977	H. Günthart	Coll. Günthart	
Kybos ludus	1♂	Switzerland, Mte. Brè	03.08.1983	L. Rezbanyai	NHMB	
Kybos ludus	1♂	Switzerland, Basel	20.07.2002	R. Mühlethaler	NHMB	
Kybos mesasiaticus	1♀	Afghanistan, Bala Murghab	02.07.1964	J. Dlabola	NMP	
Kybos mesasiaticus	1♂	Afghanistan, Bala Murghab	10.-13.07.1964	J. Dlabola	NMP	
Kybos mesasiaticus	2♂ 7♀	Mongolia, Songino	03.09.1966	J. Dlabola	NMP	
Kybos mucronatus	1♂	Bulgaria	13.08.1972	P. Lauterer	MZMB	
Kybos mucronatus	1♂	Bulgaria	16.08.1972	P. Lauterer	MZMB	
Kybos mucronatus	1♂	Czech Republic, Bohemia mer.	04.08.1973	P. Lauterer	MZMB	
Kybos mucronatus	1♂	Czech Republic, Moravia occ.	02.08.1984	P. Lauterer	MZMB	
Kybos mucronatus	1♂	France, Offendorf	10.07.1995	I. Malenovský	MZMB	
Kybos mucronatus	1♂	Poland, Karwia	25.08.1958	R. Bielawski	AMNH	"*verbae*"
Kybos mucronatus	1♂	Poland, Kazimierz	14.07.1967	I. Dworakowska	AMNH	"*verbae*"
Kybos mucronatus	2♂	Switzerland, Zernez	04.08.1973	H. Günthart	Coll. Günthart	
Kybos mucronatus	1♀	Switzerland, Zernez	04.08.1975	H. Günthart	Coll. Günthart	
Kybos mucronatus	1♂	Switzerland, Zernez	19.07.1990	H. Günthart	Coll. Günthart	On *Salix*
Kybos mucronatus	1♂	Switzerland, Zernez	19.07.1990	H. Günthart	Coll. Günthart	
Kybos mucronatus	1♂	Switzerland, Bever	09.09.2002	R. Mühlethaler	NHMB	"*verbae*"
Kybos mucronatus	2♂	Switzerland, Zuoz	?	H. Günthart	Coll. Günthart	"*verbae*"
Kybos populi	2♂	Bulgaria	20.07.1971	P. Lauterer	MZMB	
Kybos populi	1♂	Bulgaria, Harmanli	20.07.1971	P. Lauterer	MZMB	
Kybos populi	1♂	Czech Republic, Bohemia mer.	08.08.1973	P. Lauterer	MZMB	
Kybos populi	2♂ 2♀	Czech Republic, Moravia occ.	14.06.1977	P. Lauterer	MZMB	
Kybos populi	1♂	Czech Republic, Moravia occ.	14.06.1977	P. Lauterer	MZMB	
Kybos populi	2♀	Czech Republic, Nemcicky	14.06.1977	P. Lauterer	MZMB	
Kybos populi	1♂	Czech Republic, Moravia occ.	30.08.1979	P. Lauterer	MZMB	
Kybos populi	1♂	Czech Republic, Moravia centr.	10.08.1983	P. Lauterer	MZMB	
Kybos populi	5♀	Czech Republic, Brno-Mokrá	18.06.1994	P. Lauterer	MZMB	
Kybos populi	2♂	Czech Republic, Mikulov	27.07.2001	P. Lauterer	MZMB	
Kybos populi	9♂ 7♀ 1 nymph	Czech Republic, Mikulov	27.07.2001	P. Lauterer	MZMB	
Kybos populi	6♀	Czech Republic, Bilé Karpaty	20.09.2001	I. Malenovský & P. Kment	MZMB	
Kybos populi	1♀	Czech Republic, Brno	21.06.2003	R. Mühlethaler	NHMB	
Kybos populi	1♀	France, Strasbourg	22.07.1993	I. Malenovský	MZMB	
Kybos populi	2♂ 1♀	France, Strasbourg	05.08.1993	I. Malenovský	MZMB	
Kybos populi	1♀	France, Strasbourg	01.09.1993	I. Malenovský	MZMB	
Kybos populi	2♂	France, Strasbourg	13.09.1993	I. Malenovský	MZMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos populi	3♀	France, Strasbourg	13.09.1993	I. Malenovský	MZMB	
Kybos populi	1♀	France, Strasbourg	15.09.1994	I. Malenovský	MZMB	
Kybos populi	1♀	France, Strasbourg	18.09.1994	I. Malenovský	MZMB	
Kybos populi	4♀	Slovakia, Roháce-Tatliakova	14.08.1959	P. Lauterer	MZMB	
Kybos populi	14♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	
Kybos populi	1♂	Switzerland, Birsfelden	30.08.1972	H. Günthart	Coll. Günthart	
Kybos populi	1♂	Switzerland, Morel	28.08.1986	H. Günthart	Coll. Günthart	
Kybos populi	1♂	Switzerland, Basel	19.08.2001	R. Mühlethaler	NHMB	
Kybos populi	1♂	Switzerland, Samedan	06.09.2002	R. Mühlethaler	NHMB	
Kybos rufescens	2♂	Bulgaria	19.07.1971	P. Lauterer	MZMB	
Kybos rufescens	1♂	Bulgaria	20.07.1971	P. Lauterer	MZMB	
Kybos rufescens	3♂	Czech Republic, Bohemia	10.08.1973	P. Lauterer	MZMB	
Kybos rufescens	1♂	Czech Republic, Moravia mer.	19.06.1980	P. Lauterer	MZMB	
Kybos rufescens	1♂	Czech Republic, Moravia centr.	25.08.1980	P. Lauterer	MZMB	
Kybos rufescens	8♂	Czech Republic, Moravia mer.	03.06.1981	P. Lauterer	MZMB	
Kybos rufescens	16♂ 5♀	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	
Kybos rufescens	1♂	Czech Republic, Moravia or.	23.06.1983	P. Lauterer	MZMB	
Kybos rufescens	1♂	Czech Republic, Moravia or.	20.08.1984	P. Lauterer	MZMB	
Kybos rufescens	1♂	Czech Republic, Bilé Karpaty	17.06.2000	R. Mühlethaler	NHMB	
Kybos rufescens	1♂	Finland, Turku	21.07.1947	R. Linnavuori	AMNH	
Kybos rufescens	1♂	Finland, Turku	18.07.1948	R. Linnavuori	AMNH	
Kybos rufescens	1♂	France, Strasbourg	07.09.2000	I. Malenovský	MZMB	
Kybos rufescens	2♂	Germany, Weil am Rhein	27.07.2000	R. Mühlethaler	NHMB	
Kybos rufescens	1♂	Germany, Weil am Rhein	05.10.2000	R. Mühlethaler	NHMB	
Kybos rufescens	1♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	
Kybos rufescens	130♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler & P. Lauterer	NHMB	
Kybos rufescens	1♂	Germany, Weil am Rhein	23.07.2002	R. Mühlethaler	NHMB	
Kybos rufescens	4♂	Germany, Weil am Rhein	19.08.2002	R. Mühlethaler	NHMB	
Kybos rufescens	4♂	Germany, Weil am Rhein	03.06.2003	R. Mühlethaler	NHMB	
Kybos rufescens	3♂	Germany, Weil am Rhein	11.06.2003	R. Mühlethaler	NHMB	
Kybos rufescens	2♂ 7♀	Greece	04.06.1995	P. Lauterer	MZMB	
Kybos rufescens	1♂	Greece	12.06.1995	P. Lauterer	MZMB	
Kybos rufescens	2♂ 2♀	Poland, Komic	16.06.1966	I. Dworakowska	AMNH	
Kybos rufescens	2♂ 2♀	Polonia	23.06.1971	P. Lauterer	MZMB	
Kybos rufescens	4♂ 5♀	Slovakia, Palúdzká	15.07.1963	P. Lauterer	MZMB	
Kybos rufescens	7♂	Slovakia, Vazec u Strby	16.07.1963	P. Lauterer	MZMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos rufescens	4♀	Slovakia, Vazec	16.07.1963	P. Lauterer	MZMB	
Kybos rufescens	4♂ 13♀	Slovakia, Vel. Fatra-Blatnica	10.07.1976	P. Lauterer	MZMB	
Kybos rufescens	7♂ 4♀	Slovakia	10.07.1976	P. Lauterer	MZMB	
Kybos rufescens	4♂	Slovakia	11.07.1976	P. Lauterer	MZMB	
Kybos rufescens	6♂ 26♀	Slovakia	07.07.1979	P. Lauterer	MZMB	
Kybos rufescens	9♂	Slovakia	15.07.1979	P. Lauterer	MZMB	
Kybos rufescens	9♂	Switzerland, Basel	13.07.2002	R. Mühlethaler	NHMB	
Kybos rufescens	1♂	Switzerland, Basel	19.08.2002	R. Mühlethaler	NHMB	
Kybos rufescens	2♂	Switzerland, Samedan	04.09.2002	R. Mühlethaler	NHMB	
Kybos rufescens	1♂	Switzerland, Samedan	09.09.2002	R. Mühlethaler	NHMB	
Kybos rufescens	2♂ 36♀	Switzerland, Kaisten	21.06.2003	D. Wyniger	NHMB	
Kybos smaragdula	1♂	Bulgaria	08.08.1972	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Bohemia mer.	04.08.1973	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Bohemia mer.	08.08.1973	P. Lauterer	MZMB	
Kybos smaragdula	2♂	Czech Republic, Moravia occ.	22.06.1976	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Bohemia mer.	01.10.1980	P. Lauterer	MZMB	
Kybos smaragdula	7♂	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	
Kybos smaragdula	3♂	Czech Republic, Moravia or.	24.06.1982	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Brno-Staró	20.07.1982	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Moravia occ.	02.08.1984	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Moravia occ.	15.08.1984	P. Lauterer	MZMB	
Kybos smaragdula	1♀	Czech Republic, Doubravice-Klemov	07.07.1987	P. Lauterer	MZMB	
Kybos smaragdula	5♀	Czech Republic, Brnenec	25.06.1999	P. Lauterer	MZMB	
Kybos smaragdula	10♀	Czech Republic, Brno-Utechov	26.06.1999	P. Lauterer	MZMB	
Kybos smaragdula	1♂	Czech Republic, Bilé Karpaty	18.06.2000	I. Malenovský	MZMB	
Kybos smaragdula	1♂	Czech Republic, Bilé Karpaty	09.09.2000	I. Malenovský	MZMB	
Kybos smaragdula	1♂	Germany, Oberlausnitz	29.08.1998	P. Lauterer	MZMB	
Kybos smaragdula	3♂	Polonia	23.06.1971	P. Lauterer	MZMB	
Kybos smaragdula	4♂ 6♀	Romania	29.07.1971	P. Lauterer	MZMB	
Kybos smaragdula	4♂	Romania, Munti Bucegi	29.07.1971	P. Lauterer	MZMB	
Kybos smaragdula	1♀	Switzerland, Birsfelden	06.09.1971	H. Günthart	Coll. Günthart	
Kybos smaragdula	1♂	Switzerland, Basel	24.05.2000	R. Mühlethaler	NHMB	On *Betula*
Kybos smaragdula	1♂	Switzerland, Riehen	14.08.2000	D. Wyniger	NHMB	
Kybos smaragdula	2♀	Switzerland, Wildenstein	27.06.2002	R. Mühlethaler	NHMB	
Kybos sordidulus	1♂	Finland, Turku	28.07.1946	R. Linnavuori	AMNH	
Kybos sordidulus	2♂	Russia, Moskow	01.06.1963	J. Dlabola	NMP	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos strigilifer	1♂	Czech Republic, Moravia occ.	14.06.1977	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Czech Republic, Moravia occ.	30.08.1979	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Czech Republic, Moravia occ.	02.07.1980	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Czech Republic, Moravia occ.	14.06.1983	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Czech Republic, Moravia occ.	02.08.1984	P. Lauterer	MZMB	
Kybos strigilifer	5♀	Czech Republic, Vranev u Brno	06.06.1993	P. Lauterer	MZMB	
Kybos strigilifer	1♀	Czech Republic, Silesia; Uhelná	19.06.1993	H. Günthart	Coll. Günthart	
Kybos strigilifer	1♂	Czech Republic, Silesia; Uhelná	21.06.1993	I. Malenovský	MZMB	
Kybos strigilifer	1♂	Czech Republic, Bilé Karpaty	09.09.1998	I. Malenovský	MZMB	
Kybos strigilifer	1♂	Czech Republic, Bilé Karpaty	17.06.2000	I. Malenovský	MZMB	
Kybos strigilifer	1♂	Czech Republic, Brno-Reckovice	22.06.2003	R. Mühlethaler	NHMB	
Kybos strigilifer	3♂	Finland, Turku	27.06.1948	R. Linnavuori	AMNH	
Kybos strigilifer	1♂	France, Strasbourg	15.09.1994	I. Malenovský	MZMB	
Kybos strigilifer	2♂	France, La Wantzenau	10.07.1995	I. Malenovský	MZMB	
Kybos strigilifer	1♂	France, Breitenbach	07.07.1996	I. Malenovský	MZMB	
Kybos strigilifer	1♂	France, Strasbourg	06.09.1996	I. Malenovský	MZMB	
Kybos strigilifer	2♂	France, Strasbourg	07.09.1996	I. Malenovský	MZMB	
Kybos strigilifer	1♂	Germany, Weil am Rhein	27.07.2000	R. Mühlethaler	NHMB	
Kybos strigilifer	1♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	
Kybos strigilifer	1♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	
Kybos strigilifer	1♂	Germany, Weil am Rhein	09.07.2003	R. Mühlethaler	NHMB	
Kybos strigilifer	1♂	Germany, Weil am Rhein	29.07.2004	R. Mühlethaler	NHMB	
Kybos strigilifer	1♂ 1♀	Poland, Tomaszon	09.09.1967	I. Dworakowska	MZMB	
Kybos strigilifer	7♂ 3♀	Slovakia, Belanské Tatry	07.08.1967	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Slovakia	11.07.1976	P. Lauterer	MZMB	
Kybos strigilifer	1♂	Slovakia	15.07.1979	P. Lauterer	MZMB	
Kybos strigilifer	2♂	Slovenia, Tolmin	24.07.2001	H. Löcker	Coll. H. Löcker	
Kybos strigilifer	1♀	Switzerland, Meilen	13.09.1972	H. Günthart	Coll. Günthart	
Kybos strigilifer	1♂	Switzerland, Basel	25.08.2000	R. Mühlethaler	NHMB	
Kybos strobli	1♂	Czech Republic, Pouzdrany-luzní	10.06.1974	P. Lauterer	MZMB	
Kybos strobli	1♂	Czech Republic, Pouzdrany-luzní	10.06.1974	P. Lauterer	MZMB	
Kybos strobli	3♂	Czech Republic, Horní Nemcí	10.09.1998	I. Malenovský	MZMB	
Kybos strobli	1♀	Poland, Pieminy Mts.	05.07.1973	I. Dworakowska	MZMB	
Kybos strobli	1♂ 1♀	Poland, Pieniny Mts.	05.07.1975	I. Dworakowska	AMNH	
Kybos strobli	10♂	Romania	29.07.1971	P. Lauterer	MZMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos strobli	9♂	Romania, Munti Bucegi	29.07.1971	P. Lauterer	MZMB	
Kybos strobli	1♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	
Kybos strobli	4♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	
Kybos strobli	1♂	Switzerland, Genève	10.09.1919	?	MHNG	
Kybos strobli	2♂	Switzerland, Untervaz	16.06.1974	H. Günthart	Coll. Günthart	
Kybos strobli	1♂	Switzerland, Sta. Maria	02.07.1982	H. Günthart	Coll. Günthart	
Kybos strobli	1♂	Switzerland, Zernez	03.07.1982	H. Günthart	Coll. Günthart	
Kybos strobli	1♀	Switzerland, Zuoz	1987?	H. Günthart	Coll. Günthart	
Kybos virgator	10♂	Bulgaria	19.07.1971	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	25♂	Bulgaria	20.07.1971	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Bulgaria	27.07.1972	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Bulgaria	08.08.1972	P. Lauterer	MZMB	
Kybos virgator	3♂ 6♀	Bulgaria	09.08.1972	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Bulgaria	13.08.1972	P. Lauterer	MZMB	
Kybos virgator	1♂	Bulgaria	13.08.1972	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Bulgaria	16.08.1972	P. Lauterer	MZMB	
Kybos virgator	1♂ 3♀	Bulgaria	19.08.1972	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	3♂	Czech Republic, Brno-Holásky	02.08.1957	P. Lauterer	MZMB	
Kybos virgator	3♂	Czech Republic, Brno-Holásky	02.08.1957	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	2♂ 2♀	Czech Republic, Belkovice u Olomouce	20.08.1961	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	2♂	Czech Republic, Moravia mer.	06.06.1973	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia mer.	14.08.1973	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia mer.	08.10.1973	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Pasohlávký	06.06.1974	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	2♂	Czech Republic, Pouzdrany-luzní	10.06.1974	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia mer.	19.06.1975	P. Lauterer	MZMB	
Kybos virgator	1♂	Czech Republic, Moravia occ.	22.06.1976	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia mer.	24.06.1976	P. Lauterer	MZMB	
Kybos virgator	2♂	Czech Republic, Moravia mer.	24.06.1976	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia occ.	16.06.1977	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂	Czech Republic, Moravia mer.	03.06.1981	P. Lauterer	MZMB	
Kybos virgator	1♂	Czech Republic, Mor. Budejovice	23.06.1981	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	1♂ 1♀	Czech Republic, Moravia mer.	06.10.1981	P. Lauterer	MZMB	
Kybos virgator	1♂	Czech Republic, Moravia or.	23.06.1983	P. Lauterer	MZMB	
Kybos virgator	2♂	Czech Republic, Ketkovice	30.05.1993	I. Malenovský	MZMB	
Kybos virgator	1♂ 1♀	Czech Republic, Ketkovice	30.05.1993	I. Malenovský	MZMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos virgator	2♀	Czech Republic, Zblovice	12.06.1993	I. Malenovský	MZMB	
Kybos virgator	2♂	Czech Republic, Horní Nemcí	10.09.1998	I. Malenovský	MZMB	
Kybos virgator	1♂	Czech Republic, Bilé Karpaty	18.06.2000	I. Malenovský	MZMB	
Kybos virgator	2♂	Czech Republic, Bilé Karpaty	09.09.2000	I. Malenovský	MZMB	
Kybos virgator	3♂	Finland, Turku	20.07.1948	R. Linnavuori	AMNH	
Kybos virgator	1♂	France, Strasbourg	05.08.1993	I. Malenovský	MZMB	
Kybos virgator	1♂	France, Strasbourg	01.09.1993	I. Malenovský	MZMB	
Kybos virgator	2♂	France, Strasbourg	17.07.1994	I. Malenovský	MZMB	
Kybos virgator	6♂	Germany, Weil am Rhein	31.05.2002	R. Mühlethaler	NHMB	
Kybos virgator	1♂	Germany, Weil am Rhein	19.08.2002	R. Mühlethaler	NHMB	
Kybos virgator	7♂ 11♀	Greece	05.05.1995	P. Lauterer	MZMB	
Kybos virgator	2♂	Poland, Ruda	16.08.1974	I. Dworakowska	AMNH	
Kybos virgator	4♂	Polonia	23.06.1971	P. Lauterer	MZMB	
Kybos virgator	1♂	Slovakia	04.07.1976	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	2♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	aberration?
Kybos virgator	6♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	26♂	Slovakia, Slovenský Kras	09.07.1976	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	3♂	Slovakia, Oslany	10.07.1977	P. Lauterer	MZMB	"*volgensis*"
Kybos virgator	4♂	Slovenia, Hudicevec	25.06.2001	H. Löcker	Coll. H. Löcker	
Kybos virgator	1♂	Slovenia, Hudicevec	11.09.2001	H. Löcker	Coll. H. Löcker	
Kybos virgator	1♂	Switzerland, Riehen	20.06.2000	D. Wyniger	NHMB	
Kybos virgator	1♂	Switzerland, Riehen	20.06.2000	D. Wyniger	NHMB	"*volgensis*"
Kybos virgator	1♂	Switzerland, Basel	22.06.2000	R. Mühlethaler	NHMB	
Kybos virgator	2♂	Switzerland, Basel	22.06.2000	R. Mühlethaler	NHMB	"*volgensis*"
Kybos virgator	3♂	Switzerland, Basel	27.07.2000	R. Mühlethaler	NHMB	
Kybos virgator	1♂	Switzerland, Basel	27.07.2000	R. Mühlethaler	NHMB	"*volgensis*"
Kybos virgator	1♂	Switzerland, Basel	25.08.2000	R. Mühlethaler	NHMB	"*volgensis*"
Kybos virgator	4♂	Switzerland, Basel	21.05.2002	R. Mühlethaler	NHMB	
Kybos virgator	1♂	Switzerland, Basel	13.07.2002	R. Mühlethaler	NHMB	"*volgensis*"
Kybos virgator	1♂	Slovenia, Tolmin	24.07.2001	H. Löcker	Coll. H. Löcker	

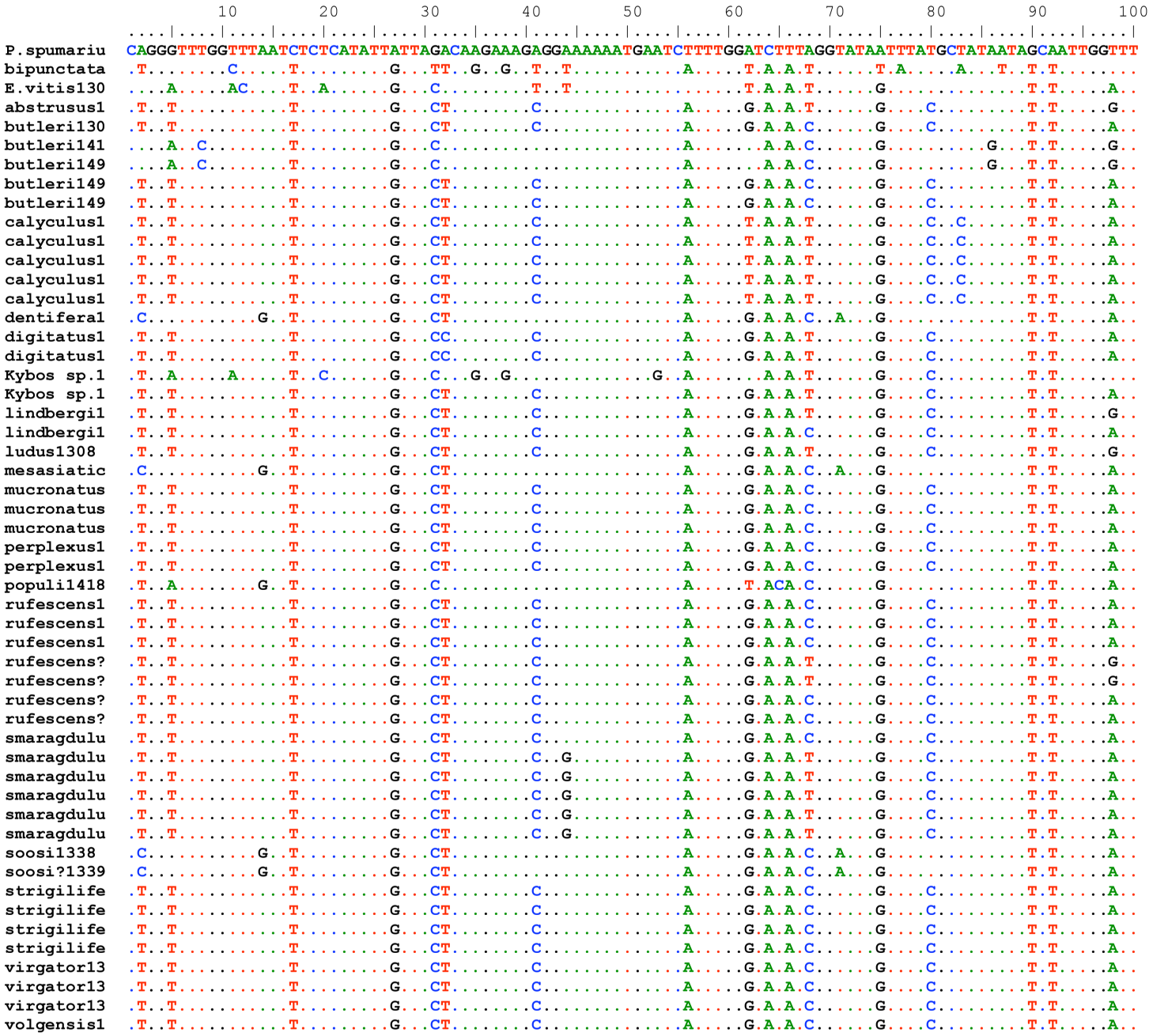
DNA Samples

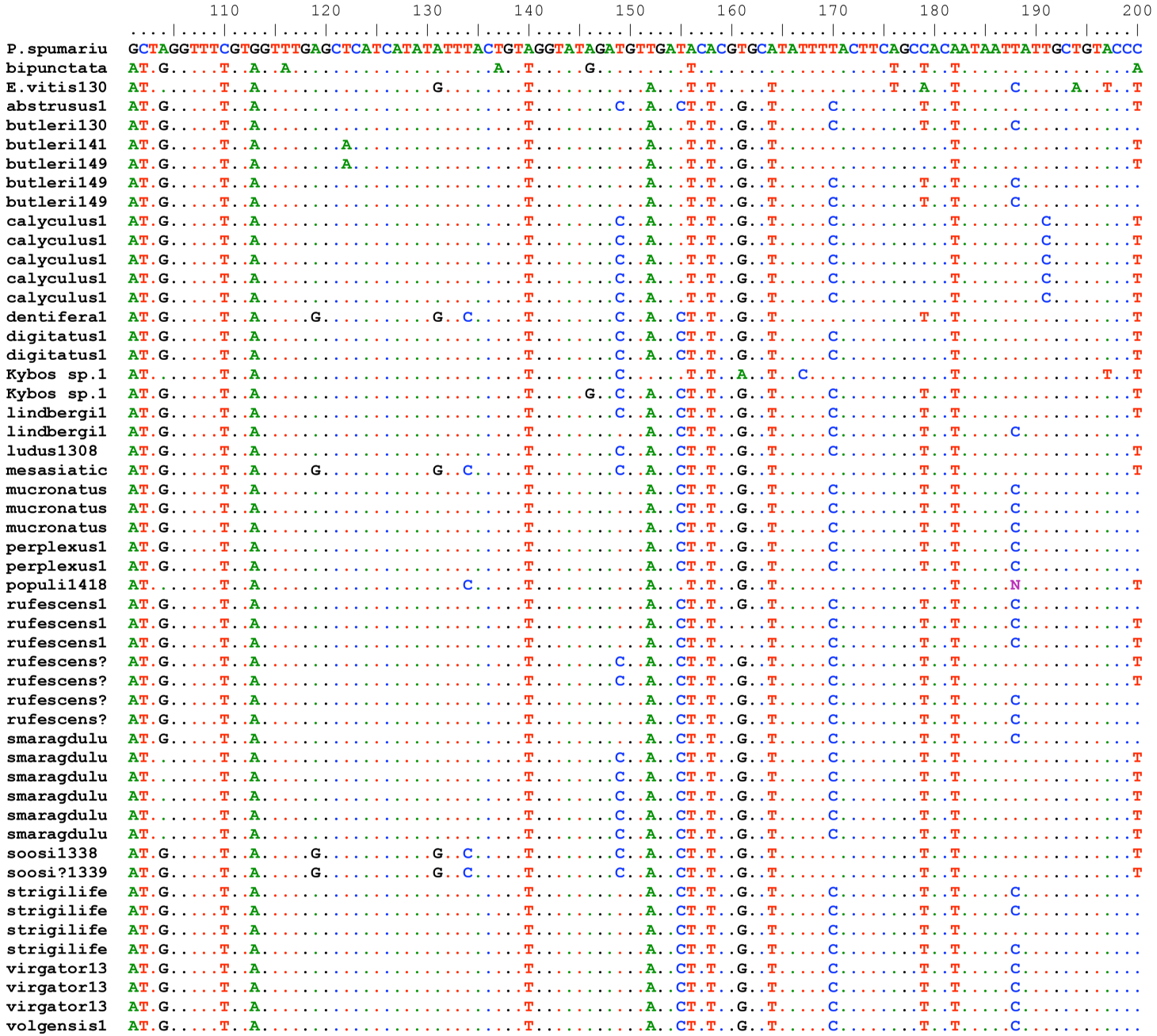
Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos abstrusus	1♀	Switzerland, Martigny	17.10.2005	Mühlethaler	NHMB	
Kybos calyculus	1♀	Czech Republic, Telnice	14.06.2005	Malenovský	NHMB	
Kybos butleri	1♂	United Kingdom, Cardiff	01.08.2005	Wilson	NHMB	
Kybos butleri	1♂	Czech Republic, Brno	24.09.2005	Lauterer	NHMB	
Kybos butleri	1♂	Czech Republic, Brno	24.09.2005	Lauterer	NHMB	
Kybos butleri	1♂	Czech Republic, Brno	24.09.2005	Lauterer	NHMB	
Kybos butleri	1♂	United Kingdom, Cardiff	01.08.2005	Wilson	NHMB	
Kybos butleri	1♂	United Kingdom, Cardiff	01.08.2005	Wilson	NHMB	only 16S
Kybos calyculus	1♂	Switzerland, Bruderholz	03.07.2005	Mühlethaler	NHMB	
Kybos calyculus	1♂	Czech Republic, Telnice	14.07.2005	Malenovský	NHMB	
Kybos calyculus	1♂	Czech Republic, Telnice	14.07.2005	Malenovský	NHMB	
Kybos dentifera	1♂	Kazachstan		Dietrich	NHMB	
Kybos digitatus	1♂	Germany, Weil am Rhein	30.08.2005	Mühlethaler	NHMB	
Kybos digitatus	1♂	Germany, Weil am Rhein	01.06.2005	Mühlethaler	NHMB	
Kybos iliensis	1♂	Kazachstan		Dietrich	NHMB	
Kybos lindbergi	1♂	Switzerland, Bruderholz	03.07.2005	Mühlethaler	NHMB	
Kybos smaragdula	1♂	Czech Republic, Telnice	14.07.2005	Malenovský	NHMB	
Kybos lindbergi	1♂	Switzerland, Samedan	03.09.2005	Mühlethaler	NHMB	
Kybos smaragdula	1♂	Czech Republic, Telnice	14.07.2005	Malenovský	NHMB	
Kybos smaragdula	1♂	Czech Republic, Brno	18.06.2005	Lauterer	NHMB	
Kybos calyculus	1♀	Luxembourg, Michelau	27.08.2005	Malenovský	NHMB	
Kybos ludus	1♂	USA, Berkeley	09.08.2005	Mühlethaler	NHMB	
Kybos mesasiaticus	1♂	Kazachstan		Dietrich	NHMB	
Kybos mucronatus	1♀	Switzerland, Samedan	03.09.2005	Mühlethaler	NHMB	"*verbae*"
Kybos mucronatus	1♂	Germany, Füssen	04.08.2003	Nickel	NHMB	
Kybos mucronatus verbae	1♀	Switzerland, Samedan	03.09.2005	Mühlethaler	NHMB	
Kybos perplexus	1♂	Switzerland, Grellingen	28.05.2005	Mühlethaler	NHMB	
Kybos perplexus	1♂	Germany, Weil am Rhein	01.06.2005	Mühlethaler	NHMB	
Kybos populi	1♂	Czech Republic, Telnice	14.06.2005	Malenovský	NHMB	
Kybos rufescens	1♂	Germany, Weil am Rhein	30.08.2005	Mühlethaler	NHMB	
Kybos rufescens	1♂	Switzerland, La Punt	13.09.2002	Mühlethaler	NHMB	
Kybos rufescens	1♀	Switzerland, Samedan	03.09.2005	Mühlethaler	NHMB	
Kybos rufescens	1♀	Switzerland, Martigny	17.10.2005	Mühlethaler	NHMB	
Kybos rufescens	1♂	Slovenia, Ljubljana	01.07.2004	Mühlethaler	NHMB	
Kybos rufescens	1♂	Germany, Weil am Rhein	01.06.2005	Mühlethaler	NHMB	

Species	Individuals	Locality	Collecting date	Collector	Depository	Notes
Kybos rufescens	1♂	Germany, Weil am Rhein	01.06.2005	Mühlethaler	NHMB	
Kybos smaragdula	1♂	Czech Republic, Dvory	26.06.2005	Malenovský	NHMB	
Kybos smaragdula	1♂	Czech Republic, Dvory	26.06.2005	Lauterer	NHMB	
Kybos smaragdula	1♂	Germany, Füssen	26.06.2003	Nickel	NHMB	only 16S
Kybos smaragdula	1♂	Germany, Füssen	19.08.2003	Nickel	NHMB	
Kybos soosi	1♂	Kazachstan		Dietrich	NHMB	
Kybos soosi	1♀	Kazachstan		Dietrich	NHMB	
Kybos sp.	1♀	USA, Muir Woods	14.08.2005	Mühlethaler	NHMB	
Kybos sp.	1♀	Kazachstan,		Dietrich	NHMB	
Kybos strigilifer	1♂	Switzerland, Grellingen	28.05.2005	Mühlethaler	NHMB	
Kybos smaragdula	1♂	Czech Republic, Bile Karpaty	24.07.2005	Malenovský	NHMB	
Kybos strigilifer	1♀	Luxembourg, Michelau	27.08.2005	Malenovský	NHMB	
Kybos strigilifer	1♂	Germany, Füssen	19.08.2003	Nickel	NHMB	
Kybos strobli	1♂	Germany, Füssen	04.09.2003	Nickel	NHMB	only 16S
Kybos virgator	1♂	Switzerland, Grellingen	28.05.2005	Mühlethaler	NHMB	
Kybos virgator	1♀	Switzerland, Samedan	03.09.2005	Mühlethaler	NHMB	
Kybos virgator	1♂	Germany, Weil am Rhein	30.08.2005	Mühlethaler	NHMB	
Kybos virgator	1♂	Switzerland, Grellingen	28.05.2005	Mühlethaler	NHMB	"*volgensis*"
Kybos virgator	1♂	Germany, Füssen	26.06.2003	Nickel	NHMB	"*volgensis*", only 16S
Empoasca vitis	1♀	Germany, Weil am Rhein	23.09.2005	Mühlethaler	NHMB	
Kyboasca bipunctata	1♂	Slovenia, Ljubljana	01.07.2004	Mühlethaler	NHMB	

Appendix 1. Material examined for morphological and molecular studies. Abbreviations: AMNH = American Museum of Natural History, USA; INER = Istituto Nazionale di Entomologia Roma, Italy; NHMB = Naturhistorisches Museum Basel, Switzerland; NMP = Národní muzeum v Praze, Czech Republic; MZMB = Moravské zemské muzeum v Brně, Czech Republic; OSU = Ohio State University, USA.

Appendix 2. COI Sequences. Number correspond to base pair positions.

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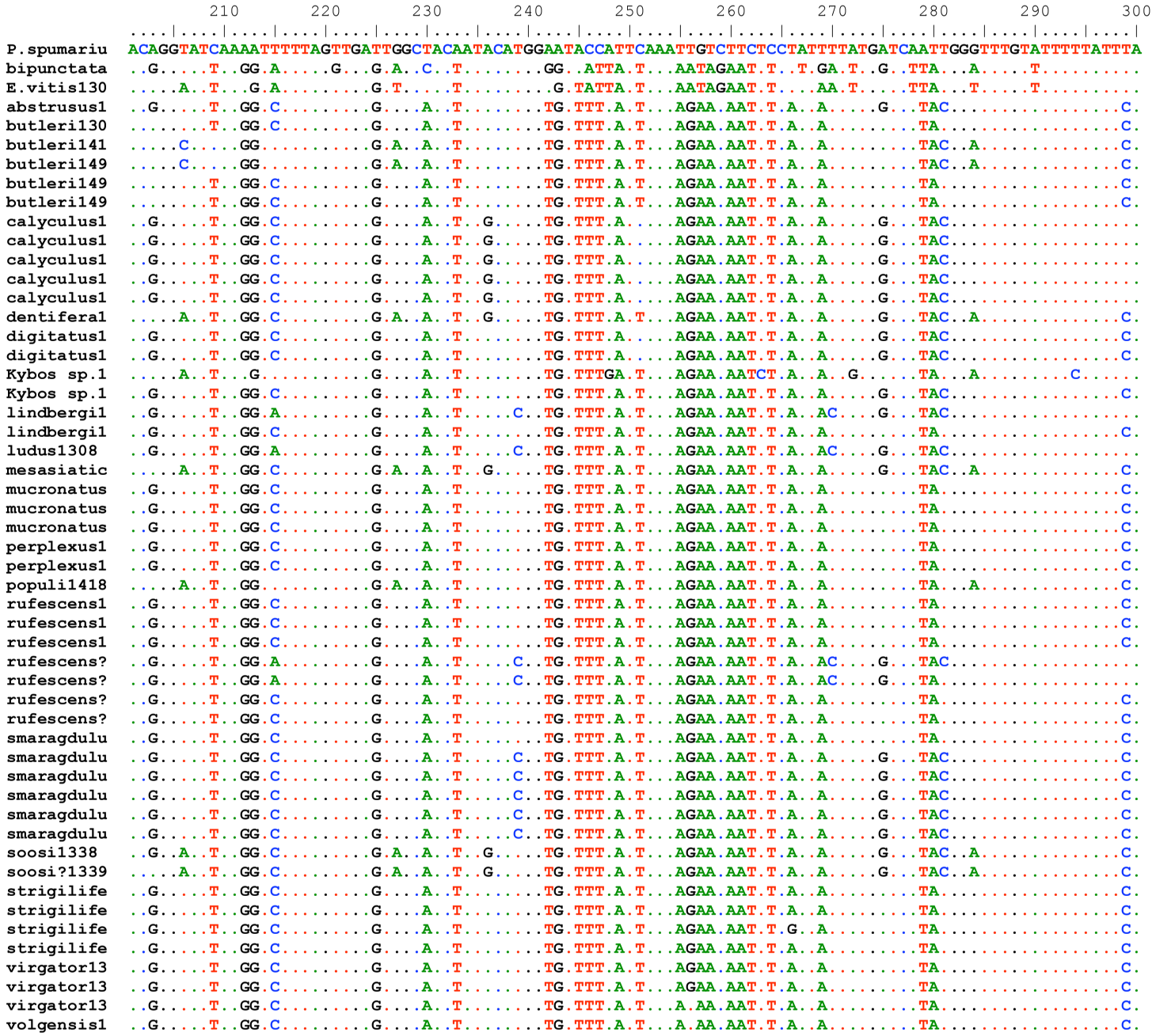
P.spumariu GCTAGGTTTCGTGGTTTGAGCTCATCATATATTTACTGTAGGTATAGATGTTGATACACGTGCATATTTTACTTCAGCCACAATAATTATTGCTGTACCC
bipunctata
E.vitis130
abstrusus1
butleri130
butleri141
butleri149
butleri149
butleri149
calyculus1
calyculus1
calyculus1
calyculus1
calyculus1
dentifera1
digitatus1
digitatus1
Kybos sp.1
Kybos sp.1
lindbergi1
lindbergi1
ludus1308
mesasiatic
mucronatus
mucronatus
mucronatus
perplexus1
perplexus1
populi1418
rufescens1
rufescens1
rufescens1
rufescens?
rufescens?
rufescens?
rufescens?
smaragdulu
smaragdulu
smaragdulu
smaragdulu
smaragdulu
soosi1338
soosi?1339
strigilife
strigilife
strigilife
strigilife
virgator13
virgator13
virgator13
volgensis1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P.spumariu ACAGGTATCAAAATTTTTAGTTGATTGGCTACAATACATGGAATACCATTCAAATTGTCTTCTCCTATTTTATGATCAATTGGGTTTGTATTTTTATTTA
bipunctata ..G.....T..GG.A.....G...G.A..C..T........GG..ATTA.T...AATAGAAT.T..T.GA.T..G..TTA...A.....T.........
E.vitis130 .....A..T...G.A.........G.T.....T.........G.TATTA.T...AATAGAAT.T....AA.T.....TTA...T.....T.........
abstrusus1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
butleri130 ........T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
butleri141 .....C.....GG...........G.A..A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TAC..A..............C.
butleri149 .....C.....GG...........G.A..A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TAC..A..............C.
butleri149 ........T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
butleri149 ........T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
calyculus1 ..G.....T..GG.C.........G....A..T..G.....TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................
calyculus1 ..G.....T..GG.C.........G....A..T..G.....TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................
calyculus1 ..G.....T..GG.C.........G....A..T..G.....TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................
calyculus1 ..G.....T..GG.C.........G....A..T..G.....TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................
calyculus1 ..G.....T..GG.C.........G....A..T..G.....TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................
dentifera1 .....A..T..GG.C.........G.A..A..T..G.....TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC..A..............C.
digitatus1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................C.
digitatus1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.....AGAA.AAT.T.A..A.....G...TAC.................C.
Kybos sp.1 .....A..T...G...........G....A..T........TG.TTTGA.T...AGAA.AATCT.A..A..G......TA...A.........C......
Kybos sp.1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
lindbergi1 ..G.....T..GG.A.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..AC....G...TAC.................
lindbergi1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
ludus1308 ..G.....T..GG.A.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..AC....G...TAC.................
mesasiatic .....A..T..GG.C.........G.A..A..T..G.....TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC..A..............C.
mucronatus ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
mucronatus ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
mucronatus ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
perplexus1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
perplexus1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
populi1418 .....A..T..GG...........G.A..A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA...A..............C.
rufescens1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
rufescens1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
rufescens1 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
rufescens? ..G.....T..GG.A.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..AC....G...TAC.................
rufescens? ..G.....T..GG.A.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..AC....G...TA..................
rufescens? ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
rufescens? ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
smaragdulu ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
smaragdulu ..G.....T..GG.C.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
smaragdulu ..G.....T..GG.C.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
smaragdulu ..G.....T..GG.C.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
smaragdulu ..G.....T..GG.C.........G....A..T.....C..TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC.................C.
soosi1338 ..G..A..T..GG.C.........G.A..A..T..G.....TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC..A..............C.
soosi?1339 .....A..T..GG.C.........G.A..A..T..G.....TG.TTT.A.T...AGAA.AAT.T.A..A.....G...TAC..A..............C.
strigilife ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
strigilife ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
strigilife ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.G..A.........TA.................C.
strigilife ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
virgator13 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
virgator13 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...AGAA.AAT.T.A..A.........TA.................C.
virgator13 ..G.....T..GG.C.........G....A..T........TG.TTT.A.T...A.AA.AAT.T.A..A.........TA.................C.
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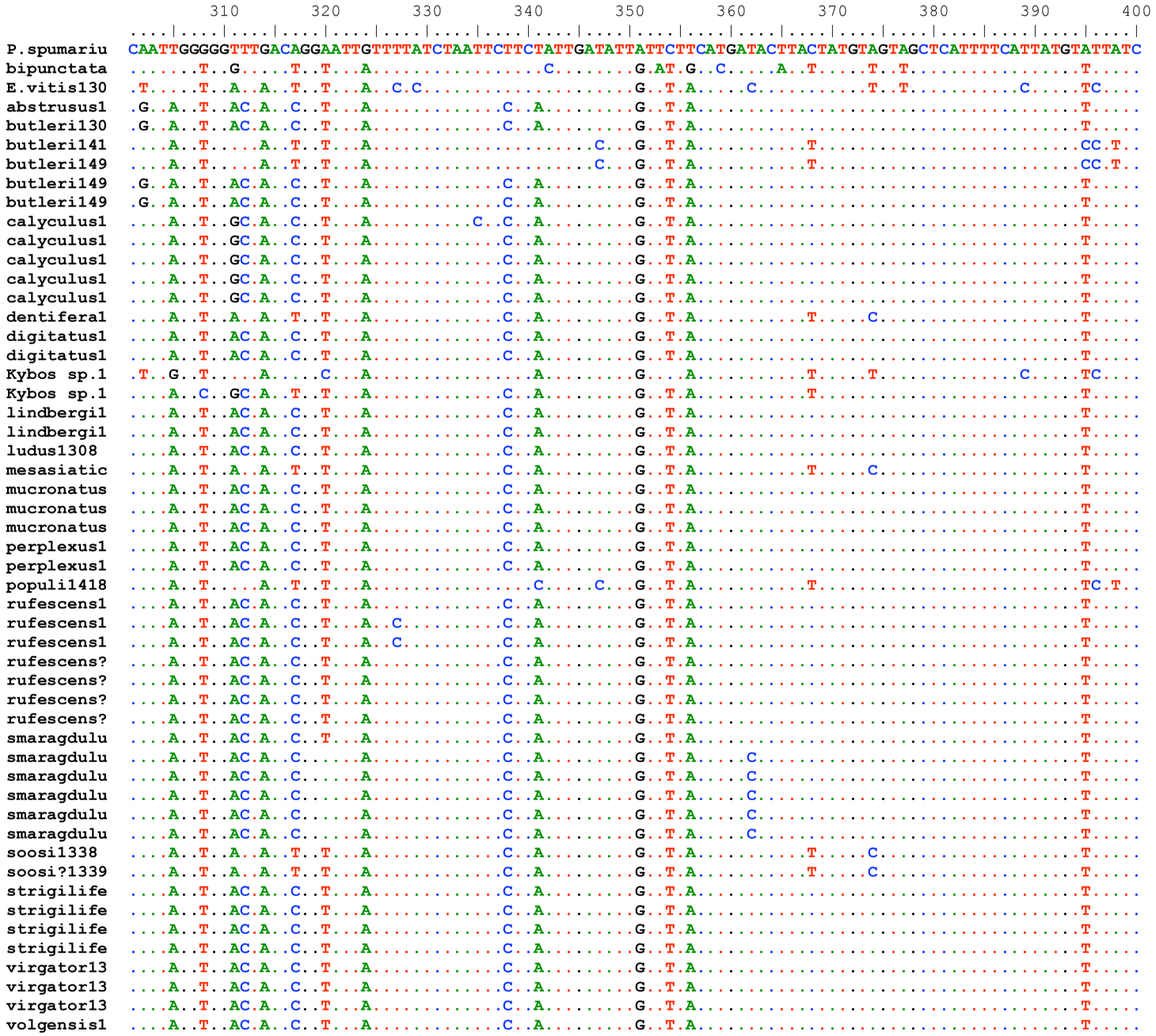
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P.spumariu CAATTGGGGGTTTGACAGGAATTGTTTTATCTAATTCTTCTATTGATATTATTCTTCATGATACTTACTATGTAGTAGCTCATTTTCATTATGTATTATC
bipunctata .....T..G.....T..T...A.....C.....G.AT.G..C.....A..T.....T..T.....T.....
E.vitis130 .T.....T..A..A..T..T...A..C.C.....G..T.A.....C.....T..T.....C....TC....
abstrusus1 .G..A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
butleri130 .G..A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
butleri141 ...A..T.....A..T..T...A.....C...G..T.A.....T.....CC.T..
butleri149 ...A..T.....A..T..T...A.....C...G..T.A.....T.....CC.T..
butleri149 .G..A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
butleri149 .G..A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
calyculus1 ...A..T..GC.A..C..T...A.....C..C..A.....G..T.A.....T.....
calyculus1 ...A..T..GC.A..C..T...A.....C..A.....G..T.A.....T.....
calyculus1 ...A..T..GC.A..C..T...A.....C..A.....G..T.A.....T.....
calyculus1 ...A..T..GC.A..C..T...A.....C..A.....G..T.A.....T.....
calyculus1 ...A..T..GC.A..C..T...A.....C..A.....G..T.A.....T.....
dentifera1 ...A..T..A..A..T..T...A.....C..A.....G..T.A.....T.....C.....T.....
digitatus1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
digitatus1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
Kybos sp.1 .T..G..T.....A.....C...A.....A.....G....A.....T.....T.....C....TC....
Kybos sp.1 ...A..C..GC.A..T..T...A.....C..A.....G..T.A.....T.....T.....
lindbergi1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
lindbergi1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
ludus1308 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
mesasiatic ...A..T..A..A..T..T...A.....C..A.....G..T.A.....T.....C.....T.....
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perplexus1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
perplexus1 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
populi1418 ...A..T.....A..T..T...A.....C.....C...G..T.A.....T.....TC.T..
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rufescens1 ...A..T..AC.A..C..T...A..C.....C..A.....G..T.A.....T.....
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rufescens? ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
smaragdulu ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
smaragdulu ...A..T..AC.A..C.....A.....C..A.....G..T.A.....C.....T.....
smaragdulu ...A..T..AC.A..C.....A.....C..A.....G..T.A.....C.....T.....
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soosi1338 ...A..T..A..A..T..T...A.....C..A.....G..T.A.....T.....C.....T.....
soosi?1339 ...A..T..A..A..T..T...A.....C..A.....G..T.A.....T.....C.....T.....
strigilife ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
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strigilife ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
virgator13 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
virgator13 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
virgator13 ...A..T..AC.A..C..T...A.....C..A.....G..T.A.....T.....
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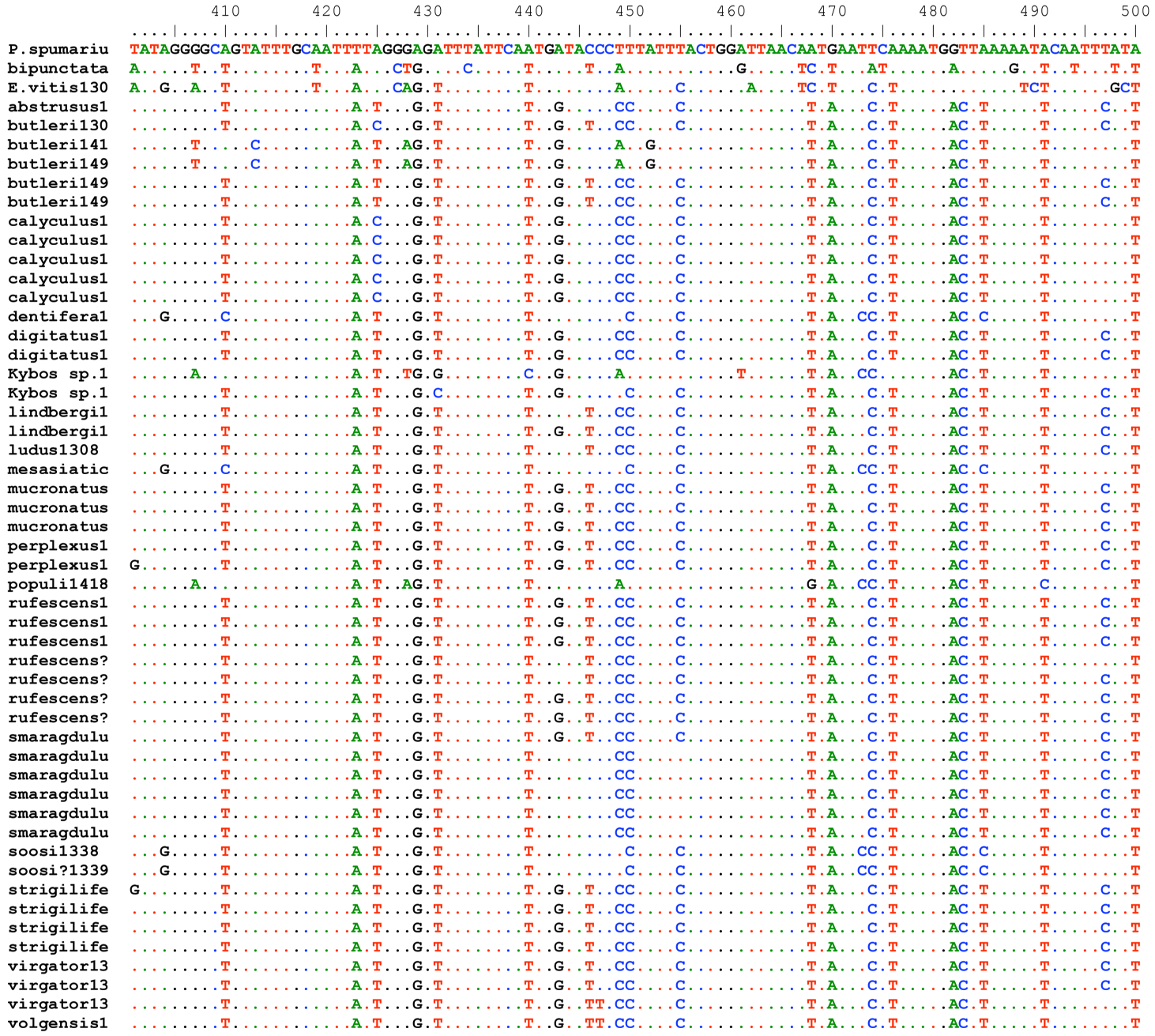
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P.spumariu TATAGGGGCAGTATTTGCAATTTTAGGGAGATTTATTCAATGATACCCTTTATTTACTGGATTAACAATGAATTCAAAATGGTTAAAAATACAATTTATA
bipunctata A.....T..T.....T...A...CTG....C.....T.....T..A.....G.....TC.T...AT.....A.....G..T..T...T.T
E.vitis130 A..G..A..T.....T...A...CAG.T.....T.....A.....C.....A....TC.T...C.T.....TCT.....GCT
abstrusus1 .....T.....A.T...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....C..T
butleri130 .....T.....A.C...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
butleri141 .....T.....C.....A.T..AG.T.....T..G.....A..G.....T.A...C.T.....AC.T.....T.....T
butleri149 .....T.....C.....A.T..AG.T.....T..G.....A..G.....T.A...C.T.....AC.T.....T.....T
butleri149 .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
butleri149 .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
calyculus1 .....T.....A.C...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....T
calyculus1 .....T.....A.C...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....T
calyculus1 .....T.....A.C...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....T
calyculus1 .....T.....A.C...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....T
calyculus1 .....T.....A.C...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....T
dentifera1 ...G.....C.....A.T...G.T.....T.....C....C.....T.A..CC.T.....AC.C.....T.....T
digitatus1 .....T.....A.T...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....C..T
digitatus1 .....T.....A.T...G.T.....T..G.....CC....C.....T.A...C.T.....AC.T.....T.....C..T
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Kybos sp.1 .....T.....A.T...G.C.....T..G.....C....C.....T.A...C.T.....AC.T.....T.....C..T
lindbergi1 .....T.....A.T...G.T.....T.....T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
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ludus1308 .....T.....A.T...G.T.....T.....T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
mesasiatic ...G.....C.....A.T...G.T.....T.....C....C.....T.A..CC.T.....AC.C.....T.....T
mucronatus .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
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mucronatus .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
perplexus1 .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
perplexus1 G.....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
populi1418 .....A.....A.T..AG.T.....T.....A.....G.A..CC.T.....AC.T.....C.....T
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rufescens? .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
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smaragdulu .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
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smaragdulu .....T.....A.T...G.T.....T.....CC.....T.A...C.T.....AC.T.....T.....C..T
smaragdulu .....T.....A.T...G.T.....T.....CC.....T.A...C.T.....AC.T.....T.....C..T
smaragdulu .....T.....A.T...G.T.....T.....CC.....T.A...C.T.....AC.T.....T.....C..T
smaragdulu .....T.....A.T...G.T.....T.....CC.....T.A...C.T.....AC.T.....T.....C..T
soosi1338 ...G.....T.....A.T...G.T.....T.....C....C.....T.A..CC.T.....AC.C.....T.....T
soosi?1339 ...G.....T.....A.T...G.T.....T.....C....C.....T.A..CC.T.....AC.C.....T.....T
strigilife G.....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
strigilife .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
strigilife .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
strigilife .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
virgator13 .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
virgator13 .....T.....A.T...G.T.....T..G..T..CC....C.....T.A...C.T.....AC.T.....T.....C..T
virgator13 .....T.....A.T...G.T.....T..G..TT.CC....C.....T.A...C.T.....AC.T.....T.....T
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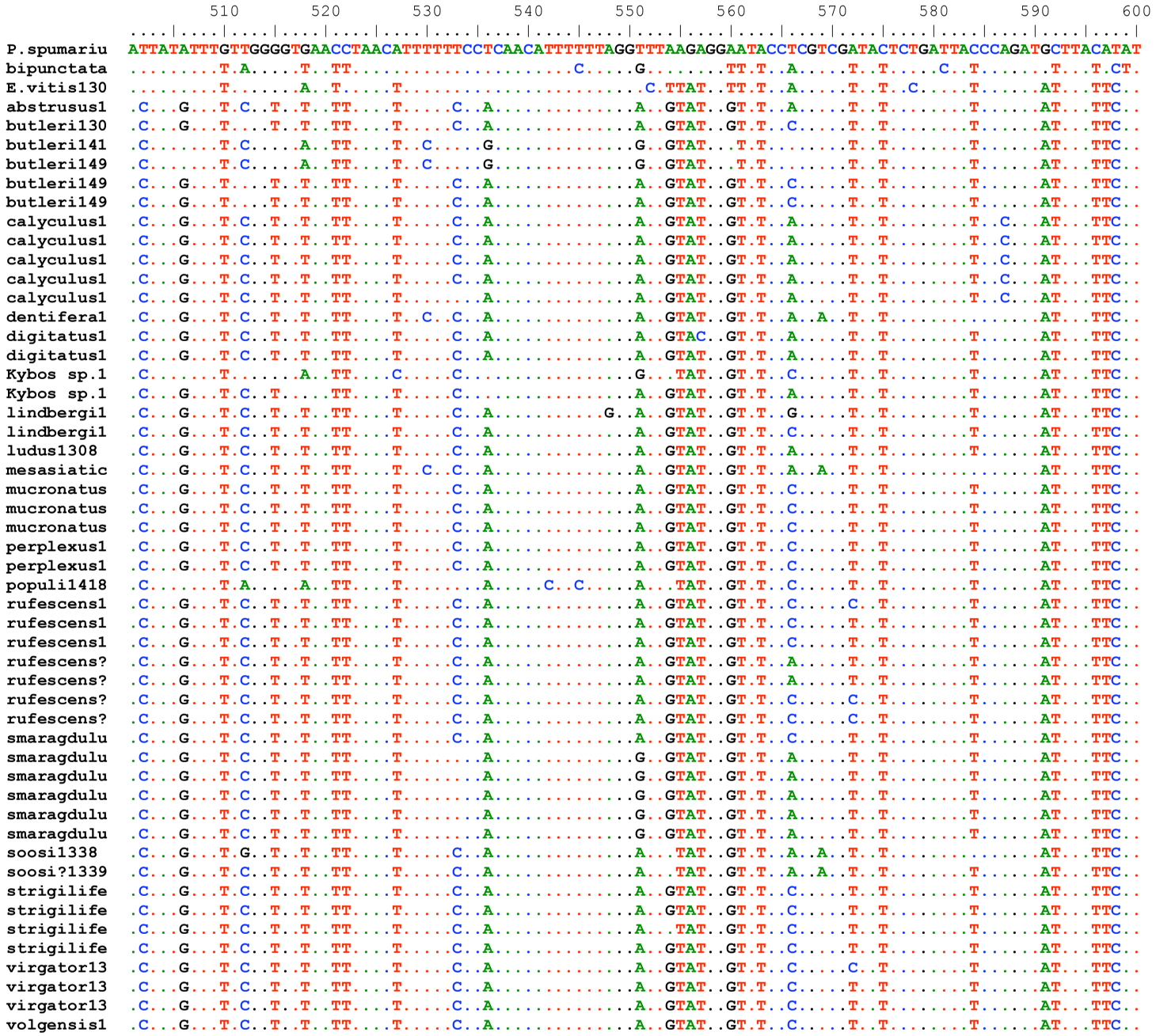
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P.spumariu ATTATATTTGTTGGGGTGAACCTAACATTTTTTCCTCAACATTTTTTAGGTTTAAGAGGAATACCTCGTCGATACTCTGATTACCCAGATGCTTACATAT
bipunctata .....T.A.....T..TT.....C.....G.....TT.T..A.....T..T.....C..T.....T...T.CT.
E.vitis130 .....T.....A..T.....T.....C.TTAT..TT.T..A.....T..T..C.....T.....AT...TTC..
abstrusus1 .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..A.....T..T.....T.....AT...TTC..
butleri130 .C...G...T....T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
butleri141 .C.....T.C.....A..TT....T..C.....G.....G..GTAT...T.T.....T..T.....T.....AT...TTC..
butleri149 .C.....T.C.....A..TT....T..C.....G.....G..GTAT...T.T.....T..T.....T.....AT...TTC..
butleri149 .C...G...T....T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
butleri149 .C...G...T....T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
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calyculus1 .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..A.....T..T.....T..C..AT...TTC..
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calyculus1 .C...G...T.C..T..T..TT....T.....A.....A..GTAT..GT.T..A.....T..T.....T..C..AT...TTC..
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smaragdulu .C...G...T.C..T..T..TT....T.....A.....G..GTAT..GT.T..A.....T..T.....T.....AT...TTC..
smaragdulu .C...G...T.C..T..T..TT....T.....A.....G..GTAT..GT.T..A.....T..T.....T.....AT...TTC..
soosi1338 .C...G...T.G..T..T..TT....T.....C..A.....A...TAT..GT.T..A..A..T..T.....AT...TTC..
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strigilife .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
strigilife .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
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strigilife .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
virgator13 .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....C..T.....T.....AT...TTC..
virgator13 .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
virgator13 .C...G...T.C..T..T..TT....T.....C..A.....A..GTAT..GT.T..C.....T..T.....T.....AT...TTC..
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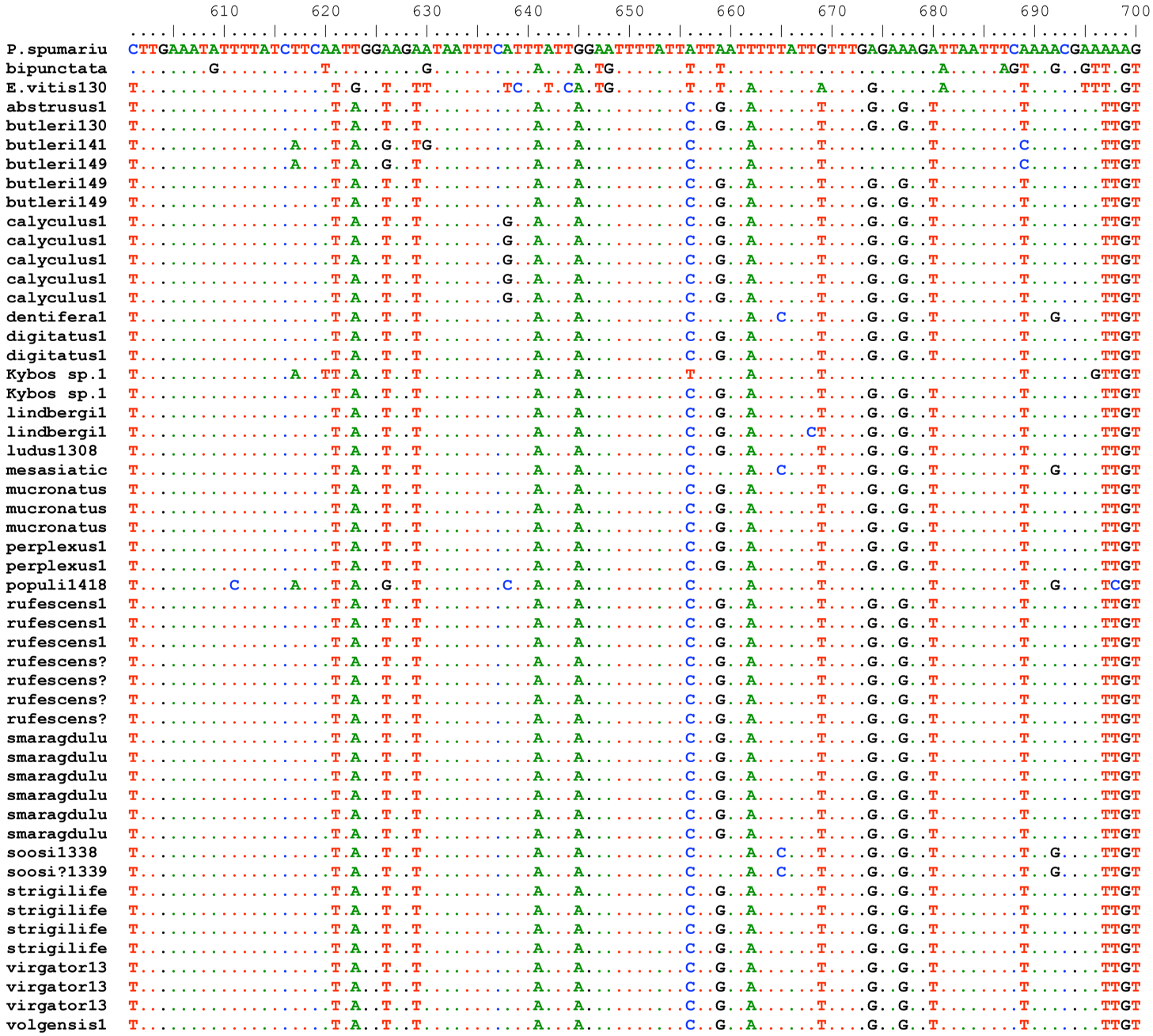
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P.spumariu CTTGAAATATTTTATCTTCAATTGGAAGAATAATTTCATTTATTGGAATTTTATTATTAATTTTTATTGTTTGAGAAAGATTAATTTCAAAACGAAAAAG
bipunctata
E.vitis130
abstrusus1
butleri130
butleri141
butleri149
butleri149
butleri149
calyculus1
calyculus1
calyculus1
calyculus1
calyculus1
dentifera1
digitatus1
digitatus1
Kybos sp.1
Kybos sp.1
lindbergi1
lindbergi1
ludus1308
mesasiatic
mucronatus
mucronatus
mucronatus
perplexus1
perplexus1
populi1418
rufescens1
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rufescens?
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smaragdulu
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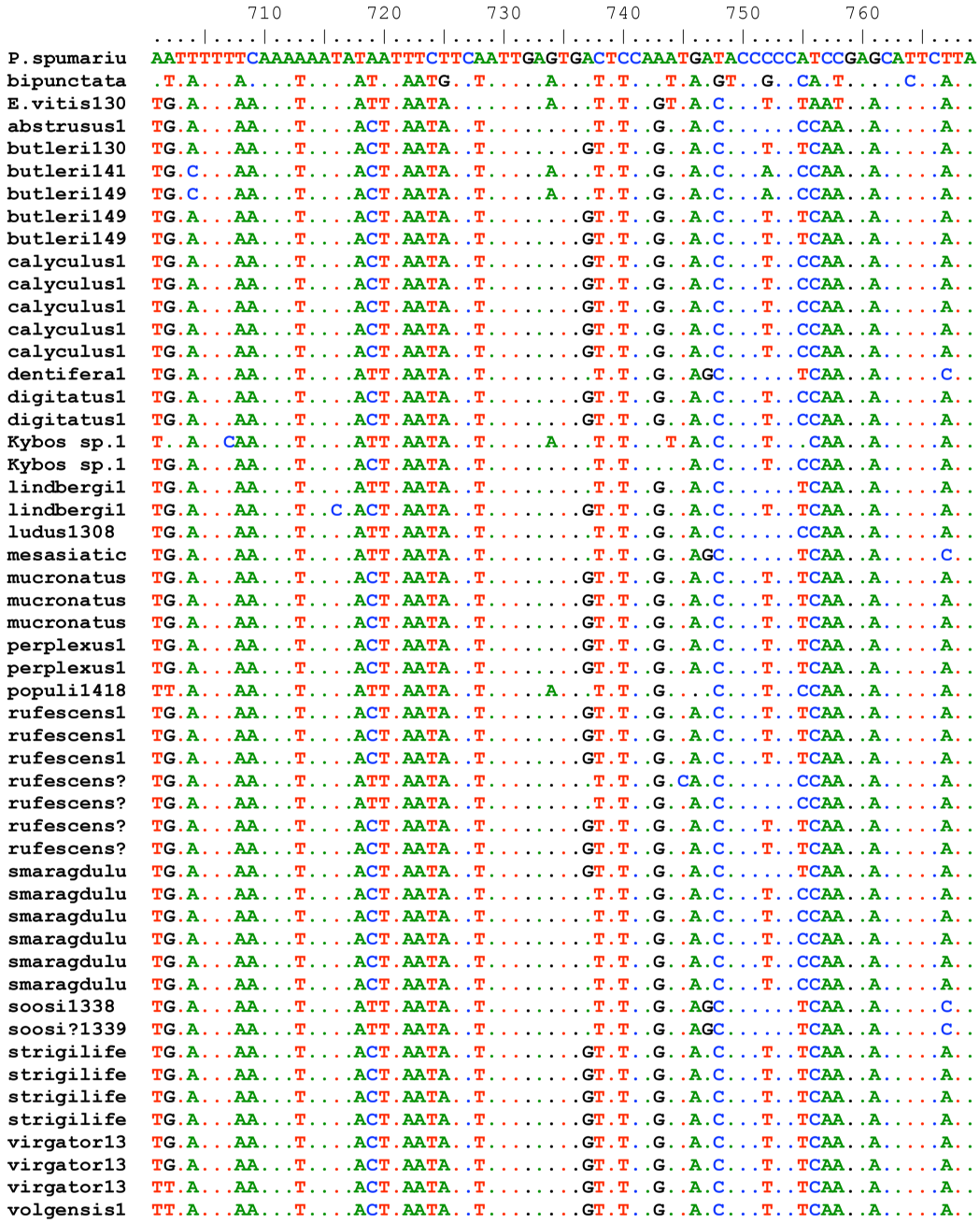
volgensis1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720
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750
760
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E.vitis130 TG.A...AA...T....ATT.AATA........A...T.T..GT.A.C...T..TAAT..A.....A..
abstrusus1 TG.A...AA...T....ACT.AATA..T.........T.T..G..A.C......CCAA..A.....A..
butleri130 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
butleri141 TG.C...AA...T....ACT.AATA..T.....A...T.T..G..A.C...A..CCAA..A.....A..
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calyculus1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..CCAA..A.....A..
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calyculus1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..CCAA..A.....A..
calyculus1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..CCAA..A.....A..
dentifera1 TG.A...AA...T....ATT.AATA..T.........T.T..G..AGC......TCAA..A.....C..
digitatus1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..CCAA..A.....A..
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lindbergi1 TG.A...AA...T..C.ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
ludus1308 TG.A...AA...T....ATT.AATA..T.........T.T..G..A.C......CCAA..A.....A..
mesasiatic TG.A...AA...T....ATT.AATA..T.........T.T..G..AGC......TCAA..A.....C..
mucronatus TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
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populi1418 TT.A...AA...T....ATT.AATA..T.....A...T.T..G....C...T..CCAA..A.....A..
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rufescens1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
rufescens1 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
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soosi?1339 TG.A...AA...T....ATT.AATA..T.........T.T..G..AGC......TCAA..A.....C..
strigilife TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
strigilife TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
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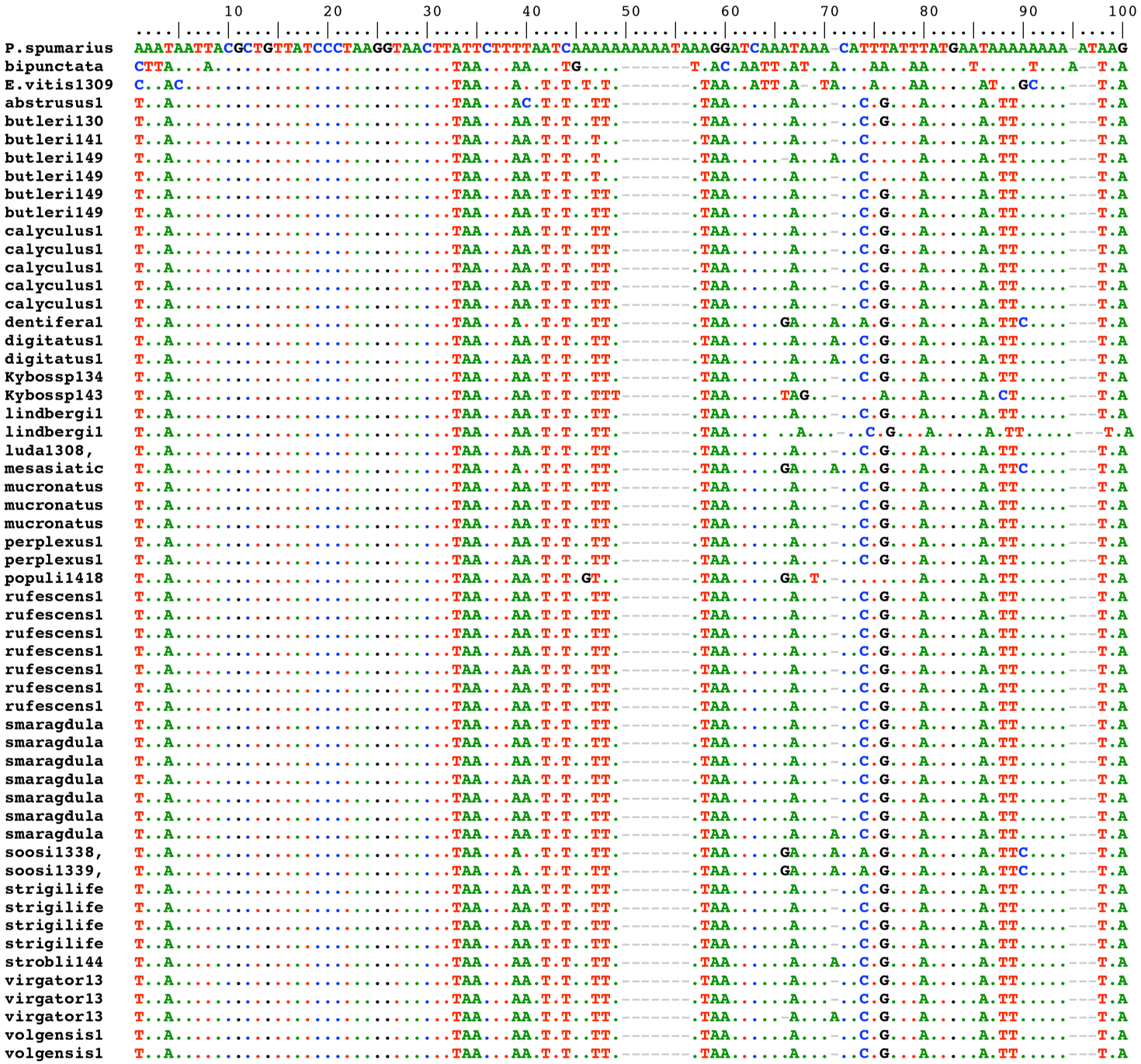
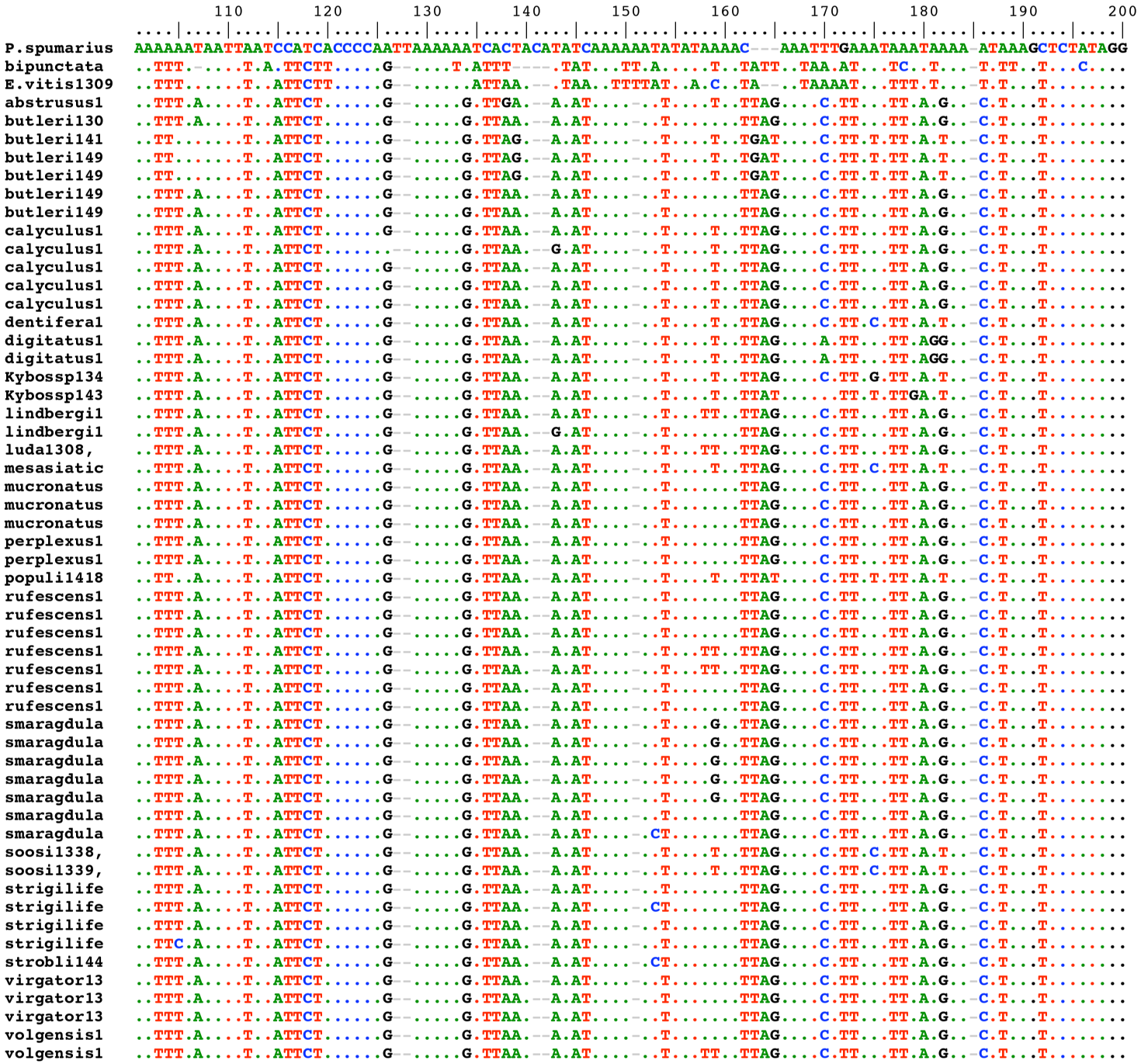
virgator13 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
virgator13 TG.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
virgator13 TT.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..
volgensis1 TT.A...AA...T....ACT.AATA..T........GT.T..G..A.C...T..TCAA..A.....A..

Appendix 3. 16S Sequences. Number correspond to base pair positions.

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bipunctata ..TTT.----.T.A.TTCTT.....G----....T.ATTT-----.TAT...TT.A.....T..TATT..TAA.AT...TC..T...-T.TT..T...C....
E.vitis1309 ..TTT.....T..ATTCTT.....G----......ATTAA.---.TAA..TTTTAT..A.C..TA---..TAAAAT...TTT.T...-T.T...T.......
abstrusus1 ..TTT.A....T..ATTCT......G----.....G.TTGA.--A.AT.....-..T....T..TTAG....C.TT...TT.A.G..-C.T...T.......
butleri130 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
butleri141 ..TT.......T..ATTCT......G----.....G.TTAG.--A.AT.....-..T....T..TGAT....C.TT.T.TT.A.T..-C.T...T.......
butleri149 ..TT.......T..ATTCT......G----.....G.TTAG.--A.AT.....-..T....T..TGAT....C.TT.T.TT.A.T..-C.T...T.......
butleri149 ..TT.......T..ATTCT......G----.....G.TTAG.--A.AT.....-..T....T..TGAT....C.TT.T.TT.A.T..-C.T...T.......
butleri149 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
butleri149 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
calyculus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....C.TT...TT.A.G..-C.T...T.......
calyculus1 ..TTT.A....T..ATTCT..........-----.G.TTAA.--G.AT.....-..T....T..TTAG....C.TT...TT.A.G..-C.T...T.......
calyculus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....C.TT...TT.A.G..-C.T...T.......
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calyculus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....C.TT...TT.A.G..-C.T...T.......
dentifera1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....C.TT.C.TT.A.T..-C.T...T.......
digitatus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....A.TT...TT.AGG..-C.T...T.......
digitatus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....A.TT...TT.AGG..-C.T...T.......
Kybossp134 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAG....C.TT.G.TT.A.T..-C.T...T.......
Kybossp143 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAT......TT.T.TTGA.T..-C.T...T.......
lindbergi1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T...TT..TTAG....C.TT...TT.A.G..-C.T...T.......
lindbergi1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--G.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
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mucronatus ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
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perplexus1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
populi1418 ..TT..A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T....T..TTAT....C.TT.T.TT.A.T..-C.T...T.......
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rufescens1 ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T...TT..TTAG....C.TT...TT.A.G..-C.T...T.......
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strigilife ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-CT.......TTAG....C.TT...TT.A.G..-C.T...T.......
strigilife ..TTT.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
strigilife ..TTC.A....T..ATTCT......G----.....G.TTAA.--A.AT.....-..T.......TTAG....C.TT...TT.A.G..-C.T...T.......
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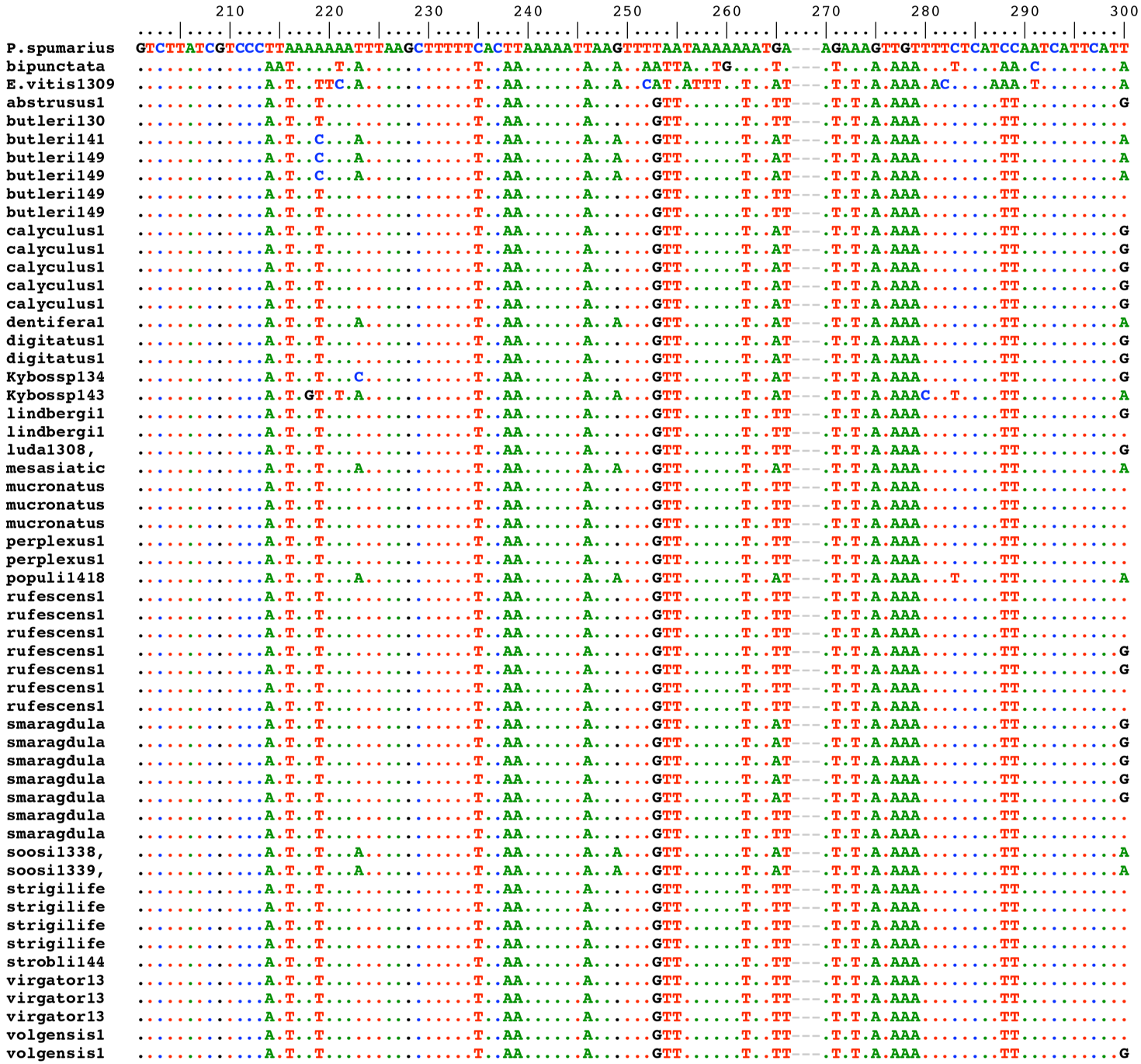
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bipunctata
E.vitis1309
abstrusus1
butleri130
butleri141
butleri149
butleri149
butleri149
butleri149
calyculus1
calyculus1
calyculus1
calyculus1
calyculus1
dentifera1
digitatus1
digitatus1
Kybossp134
Kybossp143
lindbergi1
lindbergi1
luda1308,
mesasiatic
mucronatus
mucronatus
mucronatus
perplexus1
perplexus1
populi1418
rufescens1
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rufescens1
rufescens1
rufescens1
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smaragdula
soosi1338,
soosi1339,
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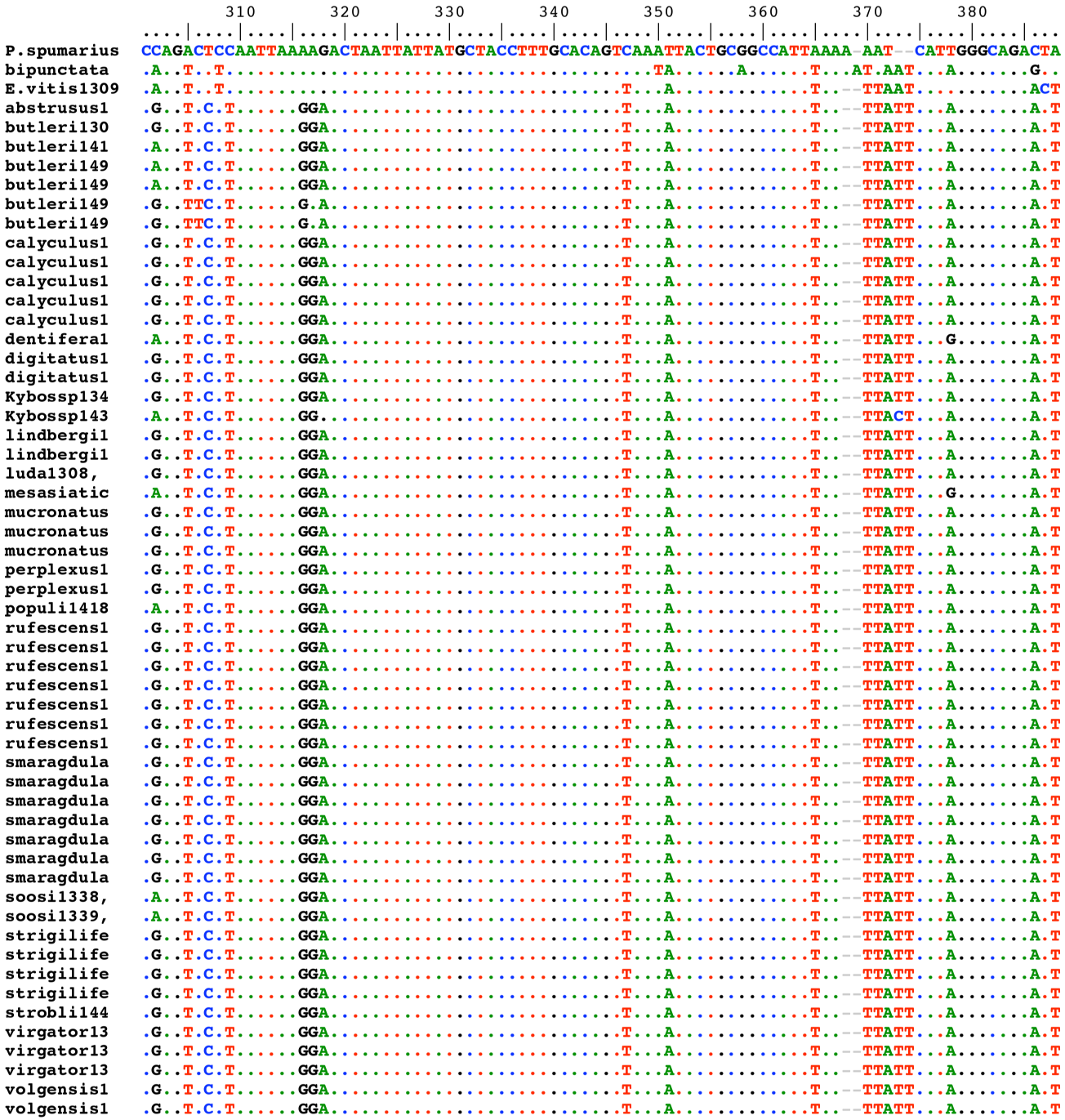
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E.vitis1309 .A..T..T.....T...A.....T..TTAAT.....ACT
abstrusus1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
butleri130 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
butleri141 .A..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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butleri149 .G..TTC.T.....G.A.....T...A.....T..TTATT...A.....A.T
butleri149 .G..TTC.T.....G.A.....T...A.....T..TTATT...A.....A.T
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calyculus1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
dentifera1 .A..T.C.T.....GGA.....T...A.....T..TTATT...G.....A.T
digitatus1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
digitatus1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
Kybossp134 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
Kybossp143 .A..T.C.T.....GG.....T...A.....T..TTACT...A.....A.T
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mucronatus .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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populi1418 .A..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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rufescens1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
smaragdula .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
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strigilife .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
strigilife .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
strigilife .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
strobli144 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
virgator13 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
virgator13 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
virgator13 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
volgensis1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T
volgensis1 .G..T.C.T.....GGA.....T...A.....T..TTATT...A.....A.T

Species	West Palaearctic	East Palaearctic	West Nearctic	East Nearctic		*Salix*	*Populus*	*Alnus*	*Betula*
abstrusus (Linnavuori, 1949)	x						x		
acodens DeLong, 1931			?	?					
aduncа DeLong, 1931			?	?					
aetnicola Wagner, 1959	x								x
alberta (Ross, 1963)			x			x			
albilacustris Tishechkin, 2002	x					x			
albolinea Gillette, 1898				x		x			
alexanderae (Ross, 1963)			x			x			
altaicus Mitjaev, 1963		x							
amicis (Ross, 1963)			x						
andresia (Ross, 1963)			x	x		x			
angustifoliae (Ross, 1963)			x				x		
annella Hartzell, 1923			x			x			
apata DeLong & Davidson, 1936			?	?					
arizona (Ross, 1963)			x				x		
aureoviridis Uhler, 1877			x			x			
auricillatus Dlabola, 1963		x							x
austriacus (Wagner, 1949)	x								x
butleri (Edwards, 1908)	x		(x)			x			
caesari (Hamilton 1972)			x						
calyculus (Cerutti, 1939)	x								x
candelabricus Dlabola, 1958	x					x			
carsona DeLong & Davidson, 1936			x				x		
cascada (Ross, 1963)			x			x	x		
chadchalicus Dlabola, 1967		x				x			
chapingo (Ross, 1963)			x			x			
chromata Davidson & DeLong, 1942			?	?					
clinata (Ross, 1963)			x	x		x			
clypeata Gillette & Baker, 1895				x					
columbiana (Hamilton, 1972)			x						
confusa DeLong & Davidson, 1936			?	?					
consecta (Ross, 1963)			x			x			
copula DeLong, 1931			x	x			x		
cornutus Dworakowska, 1968		x				x			
coronata (Hamilton, 1972)			x	x			x		
crystola (Ross, 1963)			x	x		x			
denticula Gillette, 1898			?	?					
dentifera (Logvinenko, 1980)		x				x			
digita (DeLong, 1931)			?	?					
digitatus (Ribaut, 1936)	x					x			
dissimilaris (Hamilton, 1972)			x				x		
dlabolai Dworakowska, 1973		x							
dworakowskii Mitjaev, 1980		x				x			
empusa (Hamilton, 1972)			x						
excava Davidson & DeLong, 1938			?	?					
exiguae (Ross, 1963)			x			x			
fontana (Ross, 1963)			x			x	x		
gelbata DeLong & Davidson, 1936			x				x		
gleditsia DeLong & Davidson, 1936			?	?					
gribisa (Ross, 1963)			x				x		
grosata DeLong & Davidson, 1936			?	?					

Species	West Palaearctic	East Palaearctic	West Nearctic	East Nearctic		*Salix*	*Populus*	*Alnus*	*Betula*
hartzelli Baker, 1925			x						
huanghecus (Kuoh, 1981)		x							
humilis (Ross, 1963)			x			x			
iliensis Mitjaev, 1971	x					x			
improcera (Ross, 1963)			x			x			
incida DeLong, 1931			x			x	x		
isotoma (Logvinenko, 1980)		x				x			
ivanovi (Logvinenko, 1980)	x								
jacinta DeLong & Davidson, 1936									
koreanus Matsumura, 1931		x					x		
laurifoliae Mitjaev, 1999		x					x		
limpidus (Wagner, 1955)	x					x			
lindbergi (Linnavuori, 1951)	x								x
livingstonii Gillette, 1898			x						
lucidae (Ross, 1963)			x			x			
ludus (Davidson & DeLong, 1938)	x		(x)	(x)					x
mesasiaticus (Zachvatkin, 1953)	x	x				x			
mesolinea Davidson & DeLong, 1939			?	?					
mitjaevi Dworakowska, 1976	x					x			
mucronatus (Ribaut, 1933)	x							x	
niveicolor Zachvatkin, 1953	x						x		
obrudens DeLong, 1932			?	?					
obtusa Walsh, 1862			?	?			x		
occidua (Ross, 1963)			x			x			
osborni Hartzell, 1923			?	?					
oshanini (Zachvatkin, 1953)	x					x			
ovalis (Ross, 1963)			?	?					
paraltaica (Orosz, 1996)			?	?					
patula DeLong, 1931			x			x			
pectinata DeLong, 1931			?	?					
petaluma (Ross, 1963)			x			x			
petiolaridis (Ross, 1963)			x	x?		x			
populi (Edwards, 1908)	x						x		
portola (Ross, 1963)			x				x		
pyramidialis Mitjaev, 1971	x						x		
reddina (Ross, 1963)			x			x			
rossi (Hamilton, 1972)			x				x		
rubrafacia DeLong, 1932			?	?					
rubrata DeLong & Davidson, 1936			x				x		
rubrovenosus Dworakowska, 1973	x								
rufescens Melichar, 1896	x					x			
salicis Wheeler, 1937				x					
saluta DeLong, 1931									
smaragdulus (Fallén, 1806)	x	(x) ? x	(x)	(x)				x	
soosi Dworakowska, 1976		x							
sordidulus (Ossiannilsson, 1941)	x	x	x	x		x			
sprita (Ross, 1963)			x				x		
stepposus Vilbaste, 1980		x							
strangula Davidson & DeLong, 1939			x						
strigilifer (Ossiannilsson, 1941)	x					x			
strobli (Wagner, 1949)	x							x	

Species	**West Palaearctic**	**East Palaearctic**	**West Nearctic**	**East Nearctic**		***Salix***	***Populus***	***Alnus***	***Betula***
sublactea Van Duzee, 1917			?	?					
tereholli Vilbaste, 1980		x							
tigris (Hamilton, 1972)			x				x		
topoli Zachvatkin, 1953	x	x							
transversa Van Duzee, 1917									
trifasciata Gillette, 1898			x				x		
tshagotaica Vilbaste, 1980		x							
unica (Provancher, 1890)			?	?					
velutina (Ross, 1963)			x			x			
virgator (Ribaut, 1933)	x					x			
yukonensis (Ross, 1963)			x			x			
ziona DeLong & Davidson, 1936			?	?					

Roland Mühlethaler

06.04.1974	Geboren in Basel-Stadt. Schweizer Bürger.
1994	Humanistisches Gymnasiums Basel; Maturität Typus B.
1994-2001	Studium an der Universität Basel in den Fächern Geographie; Natur-, Landschafts- und Umweltschutz; Zoologie und Meteorologie.
1999	Halbjähriges Berufspraktikum am Forschungsinstitut für Biologischen Landbau (FiBL) in Frick (Schweiz) im Fachbereich Biologischer Pflanzenschutz.
2000-2001	Diplomarbeit "Untersuchungen zur Zikadenfauna der Lebensraumtypen von Basel-Stadt (Schweiz)" am Institut für Natur-, Landschafts- und Umweltschutz (NLU) – Biogeographie unter Leitung von Prof. Dr. P. Nagel. Diplom in Geographie an der Uni Basel.
2002-2007	Dissertation unter der Leitung von Prof. Dr. P. Nagel (NLU – Biogeographie) und PD Dr. Daniel Burckhardt (Naturhistorisches Museum Basel) über die Taxonomie, Phylogenie und Biogeographie der mitteleuropäischen *Kybos*-Arten (Insecta, Hemiptera, Cicadellidae).